

Sugarcane: Its Origin and Improvement



By E. W. Brandes, *Principal Pathologist in Charge*, and G. B. Sartoris, *senior pathologist*,
Division of Sugar Plant Investigations, Bureau of Plant Industry

ONLY a few generations ago, when subsistence farming in the United States was more than a name, our forefathers made rare periodical trips to town for supplies. A bag of sugar from the West Indies was one of the few purchases for which a cash outlay was required. The frontiersman spent a considerable proportion of his limited income for this luxury, which was used for preserving fruits and to supplement the "long sweetenin'"—the sirups of maple or sorgo produced by himself or his neighbors. His bread and meat, dairy products, vegetables and fruits, even his homespun clothing, soap, candles, and often shoes were products of his own industry and that of his family.

For the majority of American families, sugar remained a large item in the budget down to very recent times. Today, even with the manifold increase in per-capita consumption, the cost is relatively insignificant. And while sugar has become a prime necessity and is recognized as a strategic military requirement in wartime, furnishing about 13 percent of the total energy we obtain from foods, modern methods of refining and handling have made it a standard for purity among foods. Sugar manufacturing is one of the most efficient modern industries, and unquestionably the most efficient agricultural industry. In quality, the product is equaled by very few others, and in quantity of raw material utilized the sugar industry is comparable to the heavy industries. A good modern plantation will harvest, transport, mill, and recover the sugar from 4,000 tons of cane every 24 hours.

The purity and cheapness of sugar is the result of concentration on problems of production and manufacture by hundreds of technologists, biologists, chemists, producers, and handlers in the industry. To consolidate the gains made and provide stabilized and adequate

supplies at reasonable prices, with due regard for a decent living for the sugar farmer, is a problem that continues to challenge the ingenuity and resources of technologists. The most important part of the task at the present time devolves upon the plant breeder.

The Significance of Plant Breeding to the Sugar Industry

IN LOUISIANA and other Southern States, further economies in production are quite possible by improvement of the sugarcane plant. Among species and varieties now available there is great variation in respect to the characters important in determining the economic usefulness of the plant. To mention only a few:

The amount of sugar and the relative proportion of sugar and other solids in the juice vary in the different kinds of cane, and the time required to reach the degree of maturity suitable for processing also varies. The relative maturity of different portions of the stalk varies, and there are great contrasts in the specific gravity, diameter, and length of stalk. Habit of growth is important, and this, together with stooling ability, offers a great range for selection. Variation is found in the response to soils, soil amendments, weather conditions, and other features of the environment. Some varieties resist deterioration better than others after a freeze or when windrowed.

Poor or gappy stands of plant cane and unsatisfactory stands of succeeding crops—the ratoons or stubble crops obtained without replanting—can usually be traced to certain specific diseases. Among the different kinds of cane there is great variation in response to infection and sometimes there is complete immunity to a disease. Among all the morphological and physiological differences observed in the different varieties of cane, the variation in response to diseases stands next in importance to variation in absolute quantity of sugar in determining the economic worth of the plant. Lack of resistance to mosaic in varieties formerly grown in Louisiana brought the industry to the brink of ruin a dozen years ago. Securing varieties resistant to the disease, after careful study and search, brought about the sensational recovery of the industry after it was forsaken as a business risk by almost all financing institutions.

This virus disease was introduced, probably about 1914, in stem cuttings of cane varieties originally from the Orient or South Pacific islands, where it was first described as injurious to the plant in the latter part of the past century. In 1919–20 workers in the Bureau of Plant Industry proved the infectious nature of mosaic and its transmission by insects and demonstrated the wide range of tolerance by different cane varieties and species. Conditions in Louisiana were favorable for rapid spread of the disease through the agency of the insect carrier, *Aphis maidis*, and production of sugar fell from an average of over 200,000 tons a year to a low of 47,000 tons, which was reached in 1926. It is estimated that losses to the sugar and sirup industries of the South due to mosaic amounted to \$100,000,000.

Attention to selection of resistant varieties suitable for commercial culture and breeding for intensification of their qualities of resistance

had begun several years before 1926 at the United States Sugar Plant Field Station near Canal Point, Fla. A world-wide search for resistant parent material marked the beginning of these efforts. Results have exceeded expectations; the sugar industry in Louisiana and the sugar and sirup industries of the other Southern States are not merely restored to former levels of production, but yields of sugar per acre are higher and are obtained at less cost than before the mosaic epidemic.

The stimulating effect of the project extended to other sugar-producing countries where mosaic was a factor, notably Puerto Rico where attention to disease-resistant varieties was emphasized by the early investigations there of workers in the Bureau of Plant Industry and later by other agencies. With continuation of breeding the forecast is for a gradual shift to better varieties for many years to come.

The plant breeder has demonstrated that he can meet the challenge of diseases and, as in this case, turn it to advantage.

WHAT IS SUGARCANE?

As the dictionary definition of sugarcane, "A tall stout perennial grass (*Saccharum officinarum*) of tropical regions, rich in sugar," is of value only for the most general usage, it would be well to delimit the term as used in this article and to point out a few of the misconceptions about sugarcane and related plants commonly met with in the United States.

Cultivated sugarcane, grown commercially in the Southern States, comprises many hybrid varieties that have resulted from natural or artificially controlled crosses of a number of species of *Saccharum*, including the species given in the dictionary, *S. officinarum*. Some of these species are not strictly tropical but range far into the North Temperate Zone. Moreover, in contrast with *S. officinarum*, they are not "stout" and are not "rich in sugar," yet owing to the lack of definitive common names in the English language they must all be admitted under the inclusive common name of sugarcane.¹

In addition to the forms cultivated in this country, there are others representing crosses between genera which, for the present at least, must also be included under the name "sugarcane." These are the forms known in Malaya as Tebu glongong and Tebu trubu and several similar ones recently collected (4)² in New Guinea, all of which appear to be natural crosses between *Saccharum* and *Erianthus*. The stems are rich in starch rather than sugar and the plants are utilized by the natives for their edible flowers.

Until special common names come into use, it will be convenient to refer to all wild or cultivated plants classified botanically under the genus *Saccharum*, or hybrids having an admixture of such plants, as sugarcane, but with modifying adjectives when necessary for clearness.

In some parts of the United States a related annual plant, sorgo or sweet sorghum—also recently crossed with sugarcane—belonging to the genus *Sorghum* is often erroneously called sugarcane, sometimes with the prefix "seeded" to indicate that it is propagated by

¹ In the Javanese language the common wild sugarcane, *S. spontaneum*, is distinguished from others by the term *glagah*, and this word has been adopted by the Netherlands resident in Java.

² Italic figures in parentheses refer to literature cited, pp. 610-611.

seeds instead of stem cuttings, as is the case with true sugarcane. Loosely used expressions such as "canebrake" have also served to add confusion to terminology in this country. A canebrake is a wild growth of reeds or canes, usually of *Arundinaria gigantea* or *Panicum hemitomon*. As no wild sugarcane is established here, it is obviously improper to use the expression in referring to sugarcane, but it is often used in a way that suggests that canebrakes are made up of sugarcane or that cultivated fields of sugarcane are canebrakes, neither of which is correct.

Typical flowers of the sugarcane are illustrated in figures 1 and 2.

PROBABLE ANCESTORS OF CULTIVATED SUGARCANE AND THEIR GEOGRAPHICAL DISTRIBUTION

The cultivated sugarcanes are probably derived from wild species of *Saccharum* (*S. spontaneum*, *S. robustum*, and unknown or extinct species), but as they sometimes appear to hybridize with other genera in nature, the latter may not be entirely excluded from consideration in tracing the origin of sugarcane. Assuming immediate descent from existing wild forms would be premature, for there is no doubt that most if not all present varieties of sugarcane are the result of extensive hybridization, the history of which has not been traced and therefore cannot be used as a basis upon which to determine questions of derivation with accuracy.³

The wild sugarcanes, *S. spontaneum* and *S. robustum*, are, so far as known, restricted to southern Asia and the chains of islands in the Indian and Pacific Oceans adjacent to southeastern Asia. The range of *S. spontaneum* seems to be much greater than that of *S. robustum*, extending from Turcomania and Afghanistan on the west to Melanesia and Taiwan on the east. Wild sugarcane of that species has been reported even from some of the small southern Pacific islands,⁴ but great antiquity of the species at either extreme of the present range is not necessarily assumed.

Sugarcane of economic usefulness has been transported by man probably for some thousands of years. When established in places specially favorable for natural reproduction by seeds, the wild forms capable of maintaining themselves in competition with other wild vegetation would be segregated from some of the hybrid cultivated forms, also transported by man, and could maintain themselves as wild plants. Doubtless this accounts for the presence of *S. spontaneum* in Tahiti, reported by John Reinhold Forster when he accompanied Capt. James Cook in 1773.

The Polynesians made many long voyages after they become skillful navigators and carried food plants, including sugarcane, to most, but not all, of the Pacific islands. It is likely that some of the long voyages were involuntary, caused by sudden storms during coast-

³ Available morphological and cytological evidence of such derivation is discussed later in this article under the genetics of sugarcane.

⁴ Explorations in these islands and Australia for the U. S. Department of Agriculture in 1935 by one of the writers resulted in the discovery of wild-growing sugarcane in Tahiti and Raiatea of the Society Islands, Efate of the New Hebrides, Viti Levu of the Fiji Islands, and New Caledonia. The sugarcane from Efate has been provisionally determined to be a variety of *S. robustum*, but the others, not yet determined, may be *S. spontaneum*. The occurrence of the latter species in Australia, reported by K. Domin in 1910, could not be confirmed, although an assiduous search was made along Harvey's Creek in northeastern Queensland, the place indicated by Domin. A. I. Bell of the Queensland Bureau of Sugar Experiment Stations and other members of the staff have also sought repeatedly for indigenous sugarcane in that region but without success. Strangely enough, it seems that in spite of the proximity of Australia to New Guinea and other natural habitats, wild cane is not found under natural conditions on that continent.



FIGURE 1.—*A*, Inflorescence of sugarcane fully expanded; *B*, lateral axis of inflorescence bearing pairs of spikelets; *C*, inflorescence in the "flagging" stage.

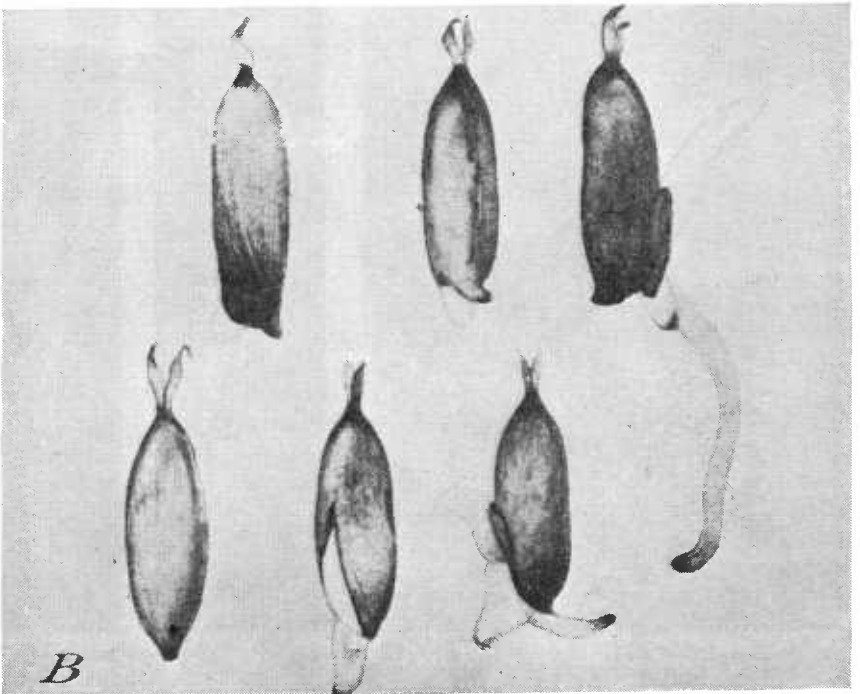
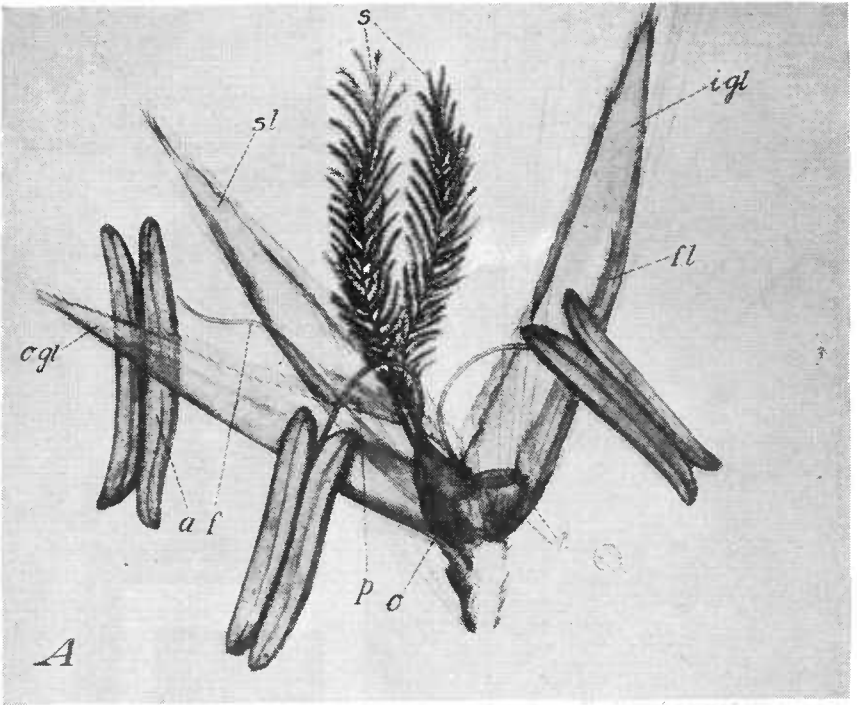


FIGURE 2.—A, Open sugarcane flower of variety U. S. 759; *i gl*, inner glume; *o gl*, outer glume; *sl*, sterile lemma; *fl*, fertile lemma; *p*, palea; *l*, lodicules; *o*, ovary; *s*, stigma; *a*, anther; *f*, filament of anther. B, Stages in the germination of sugarcane seed.

wise trips, but judging from personal observations on the food supplies carried by Papuans on coastwise trips, propagating material would be on hand to plant if new shores were reached. A more exhaustive study of the wild and cultivated sugarcane of the numerous islands of the southern Pacific, with attention to sugarcane diseases, insects, and other biological relationships, might incidentally throw light on the wanderings of the migratory races that swarmed off in successive waves from southern Asia.⁵

The other wild progenitor of sugarcane, *S. robustum*, is limited to New Guinea and adjacent islands and Celebes, so far as is known at present; but as very few observations seem to have been made on this large and striking plant, the known range may be somewhat extended when greater interest results in more attentive observations in other places.

Cultivated sugarcane was transported westward as well as eastward from the home of the wild canes, but at a later date. By successive impacts of eastern civilization, it reached southern Spain in the eighth century and was taken to the new world by Columbus on his second voyage. It is even possible with fair assurance to designate the variety of cane that reached America first and was later given the name of Creole cane or cane of the country. Importations from Spain in 1935 include this variety, a rather small, soft, yellow cane that came to us under the name Algarobena and is now grown only for chewing. It persisted in the West Indies and in Louisiana until the first years of the past century and is accurately described by Fleischmann (9). Numerous other varieties have been given the name "Caña Criolla" in the Spanish-speaking countries of the Americas, or Creole cane in English-speaking countries.

It is implied and even definitely stated in many written records extending over four centuries that sugarcane is indigenous to the New World, but there are no reliable records of finding sugarcane in places not previously visited by Europeans or in contact with Europeans. No evidence of wild sugarcane growing naturally in North America is to be found, nor of any other grass closely enough related to suggest possible descent of cane from it. It is concluded that the references to indigenous sugarcane recurring throughout the voluminous early literature on the New World⁶—for example, the report by Pere Hennepin, referred to by Labat (10), of wild sugarcane in the country around the mouth of the Mississippi River—are based on mistaken identification of other plants, as well as on mistaken conjecture or hearsay evidence often repeated by being lifted bodily from other books. The idea of independent origin of sugarcane in places other than the natural habitat of *S. spontaneum* and *S. robustum* is corroborated neither by present botanical evidence nor by reports and writings that will stand scrutiny, and it is safe to assume that the cradle of the cultivated sugarcane is the region where these two wild species are found.

⁵ The present natives of New Guinea are a mixed race, with Papuans predominating, but included are Negritos in fairly large numbers and individuals showing definite Malayan and Polynesian characteristics. The latter are too numerous to be accounted for by importation of missionary teachers from Samoa and Rarotonga during the latter part of the past century, and New Guinea may well have been the temporary home of the people who now populate Polynesia.

⁶ An unpublished manuscript by one of the present writers contains a review of the records on this subject left by early voyagers and commentators.

PRACTICES OF PRIMITIVE GROWERS OBSERVED ON A JOURNEY TO NEW GUINEA

Together with the sago, betel nut, and coconut palms, the bread-fruit and Pandanus trees, and the taro, yam, sweetpotato, and banana, sugarcane is invariably associated with primitive man in Melanesia today, especially in those almost inaccessible regions where the garden culture and food quest generally remain unchanged by contact with civilized man.

As late as 1928 (4), immense areas in the deep interior of New Guinea were found to present pictures of primeval savagery most impressive to the observers, who confidently believed that these strange



FIGURE 3.—Sugarcane and a sugarcane grower in the interior of New Guinea.

people (fig. 3) and their customs, ceremonies, and material culture represented a stage of development unique in the world today and probably not unlike that of adjacent regions 20,000 to 30,000 years ago. These areas are far from the coast and the people are not to be confused with the familiar frizzly haired coastal natives, who themselves were practically unknown until about 1850.

During this trip, opportunity for gaining knowledge of the sugarcane garden culture of the interior natives was unfortunately limited to observations lasting only a few hours or a few days at each place visited, while the observers were col-

lecting sugarcane varieties. The perishable nature of cane cuttings made long stays impossible, and the trip over New Guinea, which was made by airplane, permitted only a cursory view of the garden routine. Nevertheless, it was possible to get a fairly good idea of Papuan cane culture by piecing together these observations and what could be observed at more leisure on the coast.

The natives of all racial types in all localities visited cultivated the sugarcane. The number of villages observed was upwards of 100 and covered the entire eastern half of the island, an area equivalent to Germany and France combined. Cane was grown from the tidewater sections—where the stools in some cases were planted individually in little mounds rising a foot above sea level at high tide—to the plateau areas and mountain slopes more than a mile above sea level.

The varieties cultivated by the natives comprised an astonishing assortment, estimated at over 100 distinct kinds. Most of them were apparently unable to maintain themselves in competition with wild vegetation, judging by the appearance of sugarcane in abandoned gardens, where the jungle invariably encroached upon and smothered out the cultivated forms. Wild sugarcane was present everywhere, the *S. robustum* along watercourses and *S. spontaneum* in swamps and uplands as well. Intermediate forms, doubtless the result of natural hybridization, were found both in wet places and in situations intermittently wet and dry.

The thick-stemmed wild forms approaching the type of *S. robustum* were mostly green in color, but yellow and red varieties were also observed. The thin-stemmed wild cane, *S. spontaneum*, was quite variable in size, habit of growth, and color. Varieties were seen with red, green, and yellow stripes in various combinations, but in general the plants were of a uniform, solid green color. The color of the flesh and foliage was also variable in the wild forms, almost all colors in cultivated examples being matched in the wild sugarcane, though not in the same combinations. The small wild plants were utilized by the natives for arrow shafts and the large, woody sorts to some extent for building purposes. Sucrose is present in the juice of wild canes of both sorts, ranging from 0.5 to 7 percent.

The principal differences between these and the varieties of cultivated cane are the increased sucrose and diminished fiber content of the latter. Because of the deficiency in fiber, the cultivated canes are structurally weak and when very tall are often seen tied together and supported by long vertical poles, with overhead horizontal connecting poles extending from one stool to another (fig. 4).

The lack of fiber is desirable; the softer the cane the more it is esteemed by the natives for eating. No refining or processing of any description is practiced, and aside from ceremonial uses of varied character, the stalks of the cultivated varieties are utilized only for chewing and sucking, after they have been broken into convenient lengths.

Transition from the wild to the cultivated forms is assumed from examination of the varieties collected in native gardens, which exhibit a uniformly graduated range of forms. Just how this transition has been brought about can only be guessed, and in any particular example it is not certain whether the intermediate characters are the result of recent hybridization or previous selection of variants from the primitive forms. That variations occur through actual diversities in the germinal substance of sugarcane cannot be doubted, and when such variations are found they are readily perpetuated by vegetative reproduction.

In the case of sugarcane, therefore, it is easy to reconstruct the process by which primitive man has selected and maintained superior varieties from the profusion of wild forms everywhere at hand. It is only necessary to assume that he had powers of observation and consciousness of the significance and utility of what he observed. Observations of the present Papuans amply demonstrate that primitive man had these characteristics and used them in the field of horticulture.

As an example of the surprising perspicuity of these gardeners, who correspond to those in the Neolithic era, an incident of the trip

is worth recording. Two varieties of quite different aspect were collected in the same village. By dint of pantomime and much unintelligible shouting back and forth, it was hopefully thought that the



FIGURE 4.—Sugarcane in a Papuan garden. The canes are grown for chewing; since they are structurally weak, they are supported by upright poles connected by horizontal poles running from one stool to another.

native names of these varieties, together with names of a half dozen others in the same garden, were finally obtained. All the other names were totally different, but the two varieties mentioned bore names that were identical except for the last syllable.

The canes were attentively examined on the spot, and the minute characteristics of the buds were found to be the same, good evidence that one was merely a color variant of the other, although at first sight they had seemed strikingly different. It seemed obvious that the natives had seen the relationship, probably by observation of the stool in which the variant occurred, and when the plants were separately propagated the relation was recognized by what corresponded to scientific binomials.

No such explanation could be obtained from the natives themselves, however. Even in the case of Motuans and other coastal tribes, who now speak pidgin English, it is useless to attempt to wring from them any but the most matter-of-fact explanations, and to propound abstrusities is manifestly unfair. It is evident that what insight we gain into the processes by which utilitarian plants were developed must come from unexpected or chance evidence, as in this case, or from evidence that is indirect.

Primitive Agriculture Throws Light on the Origin of Cultivated Cane

In addition to the evidence of conscious selection of economic plants by the superior individuals among these savages, there was evidence of the development of a horticultural routine in which magic was freely mixed with agricultural practices that we flatter ourselves are highly modern.

The water requirements of sugarcane were respected and provision was made in various ways to meet them. In the tidewater section of the Kikori River and its numerous tributaries, where little dry land suitable for cane culture was available, the cane was seen planted on the tops of tubular mounds several feet high, thrown up from the mud flats by a large crustacean, not captured but seemingly a sort of glorified shrimp. Here the opportunist gardener, utilizing varieties tolerant of the slightly brackish water, found a way to accomplish both irrigation and drainage with the rise and fall of the tide. An ingenious herringbone system of drainage ditches was seen from the air in a garden on the Fly River about 100 miles from the coast. Drainage is, of course, more important than irrigation, but at times irrigation systems, including crude flumes extending across small ravines, are utilized.

Rotation of crops in the miniature gardens—few being more than an acre in size—seems not to be practiced in New Guinea, where the population is sparse and land is plentiful; but rotation of gardens, that is, abandonment of old sites in favor of new clearings laboriously made with stone axes, is universal. This has been ascribed to the fact that it requires less effort to fell trees than to fight the weeds that creep into the clearings, but the lusty growth of his taro, bananas, and sugarcane on virgin land cannot fail to have impressed the observant native.

It was noticed that the low heaps of wood ashes, left after burning the brush and logs from new clearings, were in some cases apparently selected as spots for planting, but whether by chance or because of an idea of the value of ashes as plant food could not be ascertained. The latter seems unlikely. The fight to control pests was apparently limited to taking precautions against the bush pig, wallaby, cockatoo, flying fox, rat, and other predatory animals by building fences and

by supporting and binding the canes together and wrapping them in banana leaves.

Most of the operations in the garden culture of sugarcane are so obviously rational and in keeping with good modern practice that certain backward tilling and cultivating methods stand out strongly by contrast. The garden is almost invariably disorderly as to rows and arrangement of plants, and there is no attempt at tillage. The typical garden (fig. 5) has taro, yams, bananas, sweetpotatoes, and sugarcane all growing together in the greatest confusion. The only implements of the gardener are his stone ax for clearing and the digging stick—a straight stick or pole sharpened to a point at one end. This is thrust into the soft earth, the cutting is inserted in the hole, and that is all.



FIGURE 5.—A typical Papuan garden. Cleared from the jungle with stone axes, these gardens grow taro, yams, bananas, sweetpotatoes, and sugarcane in a confused medley.

It is evident from this brief description that though the most primitive types of men in existence today practice the crudest kind of tillage, or none at all, because of lack of tools, yet they exhibit surprising familiarity with the requirements of sugarcane plants and a detailed knowledge of the plants themselves. The evidence of observation careful enough to enable them to distinguish varieties and indicate their origin by the names used seems sufficient to justify the assumption that they also consciously select better forms. Since plants that are probably the wild progenitors of cultivated cane are at hand in great profusion and variety, it is not too much to ascribe to these people the development of the cultivated sugarcane as we know it today.⁷

⁷ It has been mentioned that magic, the use of symbols or sorcerer's specifics, and procedures and observances of the weirdest and sometimes the most ludicrous or ghastly character, are woven in with the rational routine. To the natives, one is apparently as indispensable as the other. This endless variety of magical practices impresses one with the elaborate mental gymnastics of these people, to whom we are indebted for more than has been generally acknowledged. Those who may wish to pursue further the subject of Papuan magic in garden culture are referred to the exhaustive and scholarly treatise by the present Government anthropologist (20).

The varieties collected in New Guinea include some that have proved to be of great economic importance when planted commercially elsewhere. In general they are very colorful, with many striped and variegated examples, testifying to the savage's liking for brightly colored objects.

It should be emphasized that this brief description of primitive cane culture is a composite of observations among many divergent tribes and that the tribes, as well as the individuals in a particular group, differ in mental attainment and physical makeup, just as similar populations do elsewhere; also that these people have been used as illustrating the probable course of development of cane from wild to domesticated types. In most cases the latter eventually became totally unfit to compete under natural conditions with the more aggressive forms of plant life. Throughout the extensive areas in Asia where the wild forms occur, cultivated varieties doubtless arose in a like manner.

The Improvement of Varieties by the Method of Trial and Error

THE earliest records of the utilization of sugarcane by civilized races are those of the people of China and what is now British India. Within comparatively recent times many of the important commercial varieties of sugarcane in these areas were of the slender types, corresponding to the slender wild cane indigenous there; and this is true even today. The thick-stemmed tropical varieties are not newcomers in continental Asia, but they are more generally restricted to the lower latitudes and are probably migrants even there, having been brought within historic times from regions closer to the Equator, where the thick-stalked wild cane grows naturally.⁸

The part sugar has played in the stimulation of commerce between widely separated lands, the development of trade routes, the infiltration of the white race into the Tropics, and the development of tropical and subtropical countries, is a fascinating subject, but here it can only be mentioned in passing. Probably no other agricultural commodity has influenced commerce and colonization more than sugar. During the long period characterized by extension of sugarcane culture eastward and westward around the broad equatorial belt, and the subsequent gradual development of large-scale plantation methods as contrasted with the previous subsistence garden production, there seems to have been little progress in the direction of improvement of the plant itself. All this time, 2,000 years or more, there is no tangible evidence and there are no written records indicating that the possibility was thought of, although there is abundant evidence that attention was given to the adaptability of the plant to different conditions, and to improvement in cultural methods. During this period, beginning roughly with the Christian era, the attitude was one of willingness to accept the cane plant as it is.

⁸A voluminous record of sugarcane culture and manufacture of sugar in historic times has been prepared by Von Lippmann (*11*) drawn from writings of ancient chroniclers and extending down to writings of our times. The interested reader is referred to this elaborate, detailed compilation for an authentic account of sugarcane culture by the civilized races as recorded by historians, poets, and biologists.

Numerous reasons suggest themselves to account for this. There were apparently unlimited areas for expansion and there was an increasing world demand for sugar, the supply, in general, never quite reaching the demand. The energy of those engaged in the production of cane was expended in pioneering and opening new lands for cultivation. Together with the multitude of problems incidental to manufacture, transportation, and marketing, this left no time for contemplation of such abstruse ideas as the possibility of interfering with nature, or even questioning the perfection of her handiwork as exhibited in the natural or original varieties of cane. Again, the number of varieties that found their way to particular producing areas was limited. Sometimes planters in large areas relied on a single variety. This situation was not one to stimulate thought on the possible improvement of varieties. This attitude of *laissez faire*, or let things alone, continued until the early part of the nineteenth century, when the first evidence comes to light indicating that the question of improvement began to be debated.

An interesting comment by one of the more enlightened planters of the period, Leonard Wray, who had experience both in British India and in Jamaica, is worth recording here. On the subject of searching for sugarcane seed—the existence of which was doubted—with an eye to possible improvement, he says (21, p. 33):

I must own I cannot well explain why planters should be so very anxious to obtain possession of cane seed; surely they can scarcely expect to obtain a finer variety of cane than the Otaheite or Salangore!—a cane that, under favourable circumstances produces from two to three tons of dry sugar per acre!

Doubtless Wray referred not to average but to maximum yields. "Under favorable circumstances" these maximum yields, during the past decade in our own period, have been as high as 20 tons of dry sugar per acre.

At least three factors that developed during the nineteenth century are responsible for the gradual growth of the idea of planned interference with the cane plant itself, to bring about directed improvement by selection and breeding. These three factors were disease epidemics, commercial competition, and the general advance in biological science.

DISEASE EPIDEMICS—THE FIRST STIMULUS TO IMPROVEMENT

Diseases of the sugarcane are not new; quite possibly they are as old as the cultivated or the ancestral forms of cane; but for two reasons they did not result in attempts to improve sugarcane until comparatively recent times.

Under primitive conditions, when it is confined to very limited natural stands or small cultivated patches separated by miles of other vegetation, the sugarcane has been observed to be singularly free from diseases, although a variety of diseases existed in one patch or another and in exceedingly small amounts. For the most part, epidemics are due to favorable weather and other factors resulting in an increased population of disease organisms. This increased population is dependent on the number and the closeness of the host plants. If the latter are not in continuous areas but are isolated in one way or another, one of the requirements for a widespread epidemic is lacking. If there is an epidemic under these circumstances, it is local in character and spends itself without attracting much attention when the conditions

favoring the disease pass. On the other hand, where plantings of the host are massive and continuous over hundreds of square miles, the same general conditions result in enormous losses and in no uncertain way provoke thought on the cause of such disasters and the possibility of avoiding them.

During the nineteenth century and up to the present time, many of the most important producing countries reached the saturation point in sugarcane cultivation, every acre suitable for the crop—and many that are unsuitable—being utilized. Thus diseases have been more widespread and the economic losses immeasurably greater than at any time before.

Disease Relentlessly Follows the Migrations of Cane

The second reason for failing to recognize the importance of diseases and for the tardy application of thought and effort to the search for disease-resistant varieties was that frequently the cane was taken from its primeval home without disease organisms, or at least without the full complement of diseases that cane is heir to, and was established in remote places free from disease. But with increased transportation facilities and the development of a greater volume of commerce between countries, diseases relentlessly followed with subsequent cane plants or cuttings.

The most striking examples of this delayed overtaking of the cane by diseases are furnished by certain of the virus diseases, which have broken out in important commercial producing areas in the New World only in the past 30 years.⁹ After more than four centuries of cultivation in the United States the number of diseases present here is noticeably less than in India, the East Indies, the Philippines, and Australia. The great variety of diseases in the latter countries, contrasted with the relatively few diseases in all other countries of the world where sugarcane is grown, seems significant in suggesting as the place of origin of the sugarcane plant the area where the number of diseases is greatest. Indeed, if confirmation of the place of origin of sugarcane were needed, the evidence furnished by the number and variety of diseases in different parts of the world, presenting as it does a picture of successive radiating impacts of disease organisms diminishing in variety but not in intensity, would seem to supply it. For reasons that are apparent and need not be dwelt upon, the earliest migrations of cane, those to the small, widely separated South Pacific islands, are the ones in which overtaking of the cane by the diseases representing primitive associations are the longest delayed.

The earliest records of severe and widespread epidemics are concurrent with the intensive and massive cultivation of sugarcane in the nineteenth century. About 1840, in Mauritius and Reunion, there was complete failure of the Otaheite cane, which had been the backbone of the industry in those islands since its introduction from Tahiti in 1788. It is not possible to state the exact nature of the outbreak, but it seems to have appeared suddenly and to have run its course quickly. Because it was referred to as "degeneration" of the variety, an idea which has persisted in other countries to the present day, the logical course was to abandon the decadent variety and replace it with others that had not "run out," and this was done.

⁹ Because mass recovery has been observed in the case of mosaic, there is a possibility that the disease had existed in the areas before, and that these are reintroductions.

The same remedial action was taken about 1860 in Brazil, when an epidemic supposedly caused by *Bacterium vascularum* played havoc with the Otaheite variety. It was replaced by Cavangerie and other varieties selected from a considerable number brought to Brazil to reestablish the industry. The variety Otaheite was almost completely wiped out in Puerto Rico about 1872. During the course of the epidemic, it was noticed that in mixed plantings, where Rayada and Cristalina were included with Otaheite, the two former varieties were not severely attacked. Again the remedy resorted to was the substitution of varieties provided by nature.

Thus far no effort had been made to cross-breed for resistance, as infertility of the sugarcane seems to have been generally accepted. The next historic disease outbreak, however—the sereh epidemic in Java, beginning in 1880—was destined to inaugurate a new and useful tool for the plant scientist, the “nobilization” of hardy but otherwise inferior varieties by successive crossing and back-crossing with the so-called noble varieties. The latter, varieties of *Saccharum officinarum*, are as a rule susceptible to disease but are of good quality and fine, aristocratic appearance, hence “noble,” according to the Dutch scientists who introduced the English word into the Dutch language—a happy selection of a term with definite connotations.

BEGINNING OF THE IDEA OF NOBILIZING SUGARCANE

This was a gradual development, dependent upon a number of complementary discoveries and participated in by various investigators through a period of several decades. Calamities that threaten the very existence of the industry seem several times to have provided the stimulus for progress in the understanding of fundamental biological principles, and the sereh epidemic is a noteworthy example.

At the time of the outbreak, the leading variety in Java was the Zwart Cheribon (Louisiana Purple), which had little natural resistance and was the principal sufferer. The disease was specially refractory in yielding to study, and even today the etiology is obscure. It was discovered, however, that certain varieties, notably Chunnee brought from British India, were resistant. With this fact and the discovery—or more properly the presenting of convincing evidence—that certain varieties of sugarcane develop viable seeds, the means for solution of the sereh problem suggested themselves.

Chunnee is a very thin cane somewhat resembling the wild *S. spontaneum*. The planters of Java, accustomed to the large-barreled, heavy-yielding tropical varieties, were prejudiced against it. As it was totally unacceptable as a substitute for the Cheribon and Preanger, crosses were attempted between these and the Chunnee. Some of the resulting hybrids were more to the liking of planters in habit and conformation, but still somewhat disappointing.

Meantime, the industry was maintained because it was found that susceptible varieties grown in the mountains did not suffer from sereh, and seed cane from this source planted in the valleys and on the coastal plain gave rise to plants acceptable to the mills as plant cane or first-year crops. However, the ratoons arising from the stubble of these plant canes suffered severely from sereh. An expensive readjustment in methods of culture, involving transportation each year of cuttings or bibit from the higher elevations to the lowlands,

was necessary. This enabled the industry to survive, but naturally it was distasteful to those engaged in commercial cane husbandry.

A wild-growing or semiwild plant unaffected by sereh was found on the lower slopes of Tjeremai, an extinct volcano. It was presumed that this interesting plant, called Kassoer, resulted from natural crossing of Zwart Cheribon and glagah, a form of *S. spontaneum*. The possibility that it was a disease-resistant cross provided a clue for the utilization of glagah as well as Kassoer itself in crosses—a process later to become known as nobilization of the more primitive, hardy, and disease-resistant forms of sugarcane. Following this, hundreds of thousands of seedlings have been produced and carefully tested by crossings and repeated back-crossings with numerous superior but susceptible noble varieties, and the system or method of breeding has resulted in varieties not only equal but infinitely superior to the Zwart Cheribon in the days before the sereh epidemic. The successive steps in nobilizing sugarcane are illustrated in figures 6 to 10, inclusive.

The impetus given to improvement of the cane because of these disease epidemics has continued to the present day, but it cannot be claimed that they are solely responsible for such efforts in modern times. Other factors have played roles of almost equal importance.

COMPETITION BETWEEN SUGAR-PRODUCING COUNTRIES AS A STIMULUS TO IMPROVEMENT

In recent years, particularly since the close of the past century when the question of overproduction of sugar has become acute from time to time, commercial competition for markets has stimulated work on improvement of the cane plant. It is obvious that lower costs of production resulting from efficiency in the field would bring an advantage to the countries successful in producing the crop more cheaply than their competitors. This has been generally recognized and efforts toward improvement of the plant have been intensified in some quarters. At the same time it must be remembered that world overproduction brings low prices, and budgets for research suffer in the lean years, so that technological research has been retarded in the countries hardest hit during the present depression.

It may not be out of place to point out that the low world price for sugar resulting from overproduction followed hard on the close of the World War, nearly a decade before the general depression in business. In many sugar-producing countries the forced economies resulted not only in diminution of research, but in neglect of field practices long recognized as indispensable for permanent agriculture. Where research was continued, it is noticeable that it has been productive of valuable results. It may not be altogether a coincidence that practically all the knowledge we have of the principles of genetics as applied to sugarcane has been accumulated since inauguration of "tooth-and-claw" competition for the sugar markets of the world.

THE EFFECT OF GENERAL ADVANCES IN THE BIOLOGICAL SCIENCES

It cannot be said that any economic consideration supplied the motive for the revival of learning that began in the late sixteenth century. Many of the ideas on biology enunciated by the pundits of those times



FIGURE 6.—Nobilization of wild sugarcane: A variety of *Saccharum spontaneum* found in New Guinea. The canes are slender and deficient in sugar but vigorous, erect, and prolific. A good type to nobilize. Mated with the type shown in figure 7, it gives seedlings like the one illustrated in figure 8.

found confirmation in the careful researches of biologists, some of whom were doubtless stimulated by this pioneering. Although not conceived in the modern method of hypothesis, deduction, and experiment, some of the eloquent writings of Bacon (1) on the role of

science in the ideal commonwealth, in which development of new varieties of plants and animals by crossing is mentioned, may have served to crystallize and publicize ideas that provoked others to active, fruitful experimentation.

It is beyond the scope of this short survey to trace such developments, but it should be mentioned that the culture of sugarcane, the first field crop grown on a scale requiring thousands of acres in individual enterprises, at an early date engaged the attention of many men familiar with the writings of the philosophers and scientists. The recorded observations and experiments of Wray (21) indicate thoughtful consideration of many of the biological problems involved, including the possibility of improvement of cane by breeding, and he is typical of a considerable proportion of the practical planters of his day.

Wray's ideas were sometimes fanciful—for example, his attempts to stimulate the production of seed in the sugarcane by dusting the pollen of sorghum and maize on cane tassels. With luck, he might have effected the first controlled intergeneric cross with sugarcane, but he failed and was led to a wrong conclusion as to the viability of sugarcane seed. It was not an altogether

fruitless attempt, however, as the publication of his negative results directed attention to the problem, and publication of contrary views on seed production, based on observations by other planters, soon followed.

An eagerness to keep abreast of scientific thought in agriculture characterized the sugarcane planters long before the days of cooperative endeavor and the beginning of research endowed by the State. This appreciation of the advantages to be gained by attention to the general advances of science played an important part in preparing the way for recognition of the value of breeding.

Research Institutions Enter the Picture

The stimulation due to scientific advances was partly responsible for the formation of associations of planters and agricultural societies. The inauguration of research institutions was an outgrowth of the meetings of groups which gathered to discuss problems and extend



FIGURE 7.—Nobilization of wild sugarcane; cultivated sugarcane, a variety of *Saccharum officinarum* with high sugar percentage found in New Guinea. Note the large stalks, relatively few in number, contrasted with the wild variety illustrated in fig. 6. Unlike the latter it has little resistance to most diseases.



FIGURE 8.—Nobilization of wild sugarcane: A hybrid resulting from crossing the types shown in figures 6 and 7. This is the first step in nobilization of a wild cane. The hybrid is vigorous, prolific, and of excellent habit but of no commercial usefulness because of low sucrose percentage.

information by means of reports and periodicals. Beginning in the nineteenth century, these institutions provided the means for sustained attack on problems of cane husbandry that formerly had to be chinked into the crevices of an overburdened commercial routine in the case of most planters. Not less than 100 such institutions have

come into existence, about half being privately supported by individual estates or plantations and the rest by governments or associations of planters. Only a few of the experiment stations, public and private, which give some attention to sugarcane improvement have devoted to breeding the persistent effort necessary for the production of valuable varieties, and still fewer have contributed to methods and principles in breeding sugarcane.

The stations which, if not the earliest of those giving attention exclusively to cane, at least carried on investigations acknowledged to mark the beginning of sugarcane breeding were located in Java and Barbados. They were established almost simultaneously and began work in 1886. Two stations in Java, those at Tegal and Kagok, date from that year and the Proefstation Oost Java at Pasoeroean from the year following. These were all privately supported by associations of growers. The one in Barbados was a Government institution, attached to the Boys' Reformatory School at Dodds in order to utilize the labor available there, and was called the Botanic Station.

Up to the time of establishing these stations the seed of sugarcane had not been figured or described by botanists, although the flower had been excellently described and illustrated. The existence of functioning or viable seed was doubted by responsible and careful observers

who had sought for them in vain. It is true that reports on the natural occurrence of seedlings in Barbados, Java, and elsewhere had been made for many years, but with no evidence of actual handling of the seed or planting it, and claims respecting these chance natural seedlings were usually met with ridicule. In the light of present knowledge of the development of flower and seed in sugarcane it is not difficult to understand this early skepticism. The varieties grown commercially bloomed irregularly and the percentage of the minute seeds capable of germinating was extremely small.

In 1889 Dr. Benecke reported on work which showed clearly that Dr. Soltwedel had observed the occurrence of true seed and its germination in 1887 at the Central Java Experiment Station in Semarang.



FIGURE 9.—Nobilization of wild sugarcane: Cultivated sugarcane. A variety of *Saccharum officinarum* formerly grown commercially in Louisiana. It is subject to injury by disease but is of good quality and early in maturing. The latter characteristic is important in Louisiana, so the variety is desirable for further improvement of the hybrid shown in figure 8.

In the same year J. B. Harrison reported on similar observations made by him and J. R. Bovell early in 1888 at the botanic station in Barbados. The 6 months separating the time of these independent observations, reported the same year, is attributable to the fact that in Java, south of the Equator, sugarcane blooms from May to July, and in Barbados, in the Northern Hemisphere, it blooms from November to January.

The independent researches of these two groups of investigators were of great significance to the cane industries of their respective countries, and directly or indirectly were of far-reaching importance in many other important cane-producing countries. In Java they laid

the groundwork for an increase in the production of sugar per unit of area amounting to over 300 percent in the period from 1885 to 1925, and this cannot be said to represent the maximum yield possible.

Not all of the increase can be credited to the improvement of varieties by breeding. In fact, from the year 1844 to the beginning of the period when systematic breeding began, a similar increase in yield had already been accomplished by other means. The total increase in yield from 1844 to the present time is close to 1,000 percent. Breeding has been the main factor during the past four decades, however, and the investments in breeding studies are acknowledged to have paid handsome dividends.

Certain important sugar countries, notably Cuba, have not taken advantage of the possibilities in breeding cane, and the improvement of the cane plant by scientific methods has lagged there.



FIGURE 10.—Nobilization of wild sugarcane: A hybrid obtained by crossing the variety illustrated in figure 9 with the hybrid type shown in figure 8. The result is a superior high-yielding economic plant, relatively high in sugar percentage, relatively early in maturity, and of good habit of growth. The materials and steps in producing this seedling are illustrated in figures 6 to 10.

Modern Methods of Improving Sugarcane and Their Results

PRIOR to the establishment of the first sugarcane-breeding stations in Java and Barbados, the improvement of sugarcane was effected by means of selection from the world material. In the

Tropics selection was confined to the varieties of *Saccharum officinarum*, or noble canes. Until recent years most of the sugarcanes of commerce were varieties of this species—Creole, Otaheite, Black Chiribon, and so forth. In the subtropical areas of India and Indochina, commercial varieties were selected from *S. barberi* (the Indian canes such as Chunnee, Mungo, Kansar) and from *S. sinense* (the varieties Uba, Kavangire, Cayana, and so forth, more commonly known as Japanese canes). These varieties have never had as wide distribution as those of *S. officinarum*, but they have played a part in the modern improvement of sugarcane, and they have been used in certain areas to save the sugar industry when the noble canes were stricken by disease.



FIGURE 11.—Wild sugarcane, a variety of *Saccharum robustum* found in New Guinea. Representatives of this species have been found in Celebes and more recently (1935) in the New Hebrides. The usefulness of *S. robustum* in breeding sugarcane has not yet been demonstrated, but by crossing and back-crossing with "noble" varieties, some seedlings of immense size and fair quality have been produced. Contrast the size of this plant with that of the wild variety shown in figure 6.

Besides the cultivated species, two wild species are used in the modern improvement of sugarcane by hybridization—*Saccharum spontaneum* and *S. robustum*. The former is the more important because its hybrid seedlings are adapted to a wide range of soil and climatic conditions, and from it are inherited immunity to mosaic and smut, diseases of major economic importance. The actual value of *S. robustum* (fig. 11) is not known because it is a new species collected from the wilds of New Guinea in 1928 by E. W. Brandes and J. Jeswiet, so that there has not been sufficient time to test it. Its hybrid seedlings produced at Canal Point, Fla., and in Australia and Hawaii show promise, and there is no doubt that in combination with other species it will be of value in breeding new types of commercial sugarcane.

TABLE 1.—General characteristics of sugarcane species

Species	Sucrose content	Maturity	Fiber content	Stalk girth	Width of leaves	Adaptability	Reaction to—			Remarks
							Sereh	Mosaic	Smut	
<i>S. officinarum</i> ..	High.....	Variable ..	Low.....	Large.....	Wide.....	Confined to Tropics.	Susceptible ..	Susceptible ..	Moderately susceptible.	Some varieties resistant to Fiji disease and gummosis; cultivated species.
<i>S. sinense</i>	Intermediate.	Early.....	High.....	Medium to slender.	Medium to narrow.	Wide.....	Immune.....	Some varieties susceptible.	Susceptible.....	Cultivated species; great vigor.
<i>S. barberi</i>	do.....	do.....	do.....	do.....	do.....	Temperate and sub-Tropics.	do.....	Susceptible but tolerant.	Moderately susceptible.	Do.
<i>S. spontaneum</i> ¹ ..	Very low.....	Very high.	Very slender.....	Narrow.....	Wide.....	do.....	Immune.....	do.....	Wild species; great vigor; susceptible to downy mildew and leaf spot.
<i>S. robustum</i> ¹ ..	Low.....	do.....	Medium to large; great length.	Medium.....	Natural range confined to the Tropics but appears to be adapted to a wide range of conditions.	Undetermined	Susceptible ..	Undetermined ..	Wild species; great vigor.

¹Only *S. spontaneum* and *S. robustum* are able to maintain themselves in a wild state.

The world material, comprising hundreds of varieties, is grouped under five species. The species and their general characteristics are listed in table 1.

Regarding characteristics not included in table 1, it may be said in general that the varieties of *S. officinarum* are susceptible to most of the major diseases and are not adapted to adverse conditions of soil and climate.

The varieties of *S. sinense* are immune to sereh disease but do not react uniformly to mosaic, some being susceptible and others apparently immune. These varieties are very susceptible to smut. They possess great vigor and are adapted to a wide range of conditions.

The varieties of *S. barberi* are of about the same vigor as those of *S. sinense*, and are adapted to culture under the more severe conditions of the sub-Tropics. They are immune to sereh but susceptible to mosaic; however, these varieties are not severely injured by this disease but are tolerant of it.

The varieties of *S. spontaneum* are immune to mosaic and sereh, but are attacked by smut, downy mildew, and several leaf spots. They are exceedingly vigorous, however, and are capable of maintaining themselves in a wild state.

S. robustum is similar to *S. spontaneum* in that it can maintain itself in a wild state, but it is susceptible to mosaic. However, it has better agronomic characteristics than the other wild canes.

From this review of the general characteristics of the sugarcane species, it is obvious that for hybridization with noble varieties, *S. spontaneum* should be preferred because of its immunity to disease and great vigor. Next to it are *S. barberi* and *S. robustum*. *S. sinense* has desirable characteristics, but as its progenies are usually very poor it has been used very little in breeding. The true value of the species is not known. In a few combinations it has given seedlings of promise. As knowledge about it increases, it is very probable that it will prove to be of value in breeding new types of seedlings.

The natural species and varieties of sugarcane and the hybrid varieties available for breeding work, with their characteristics, are given in the appendix (pp. 612-624).

PECULIARITIES OF SEXUAL REPRODUCTION IN SUGARCANE

In commercial practice sugarcane is propagated asexually by means of cuttings of the stalk. These cuttings are commonly called seed cane. When a variety is propagated by cuttings it remains constant and true to type. In contrast to commercial practice, reproduction in breeding sugarcane is by sexual means from true seed. As in apples, potatoes, and some other plants, no variety breeds true from seed. Every seed produces a distinct variety.

The inflorescence of sugarcane is an open-branched panicle. There are hundreds of minute flowers in a panicle. The flowers are in pairs, one sessile (without a stalk), the other pedicellate (attached to a stalk), both perfect and awnless (fig. 1).

While the flowers of all varieties are perfect, with both male and female organs (fig. 2), many of the varieties do not produce fertile pollen. Thus the varieties may be divided into two general classes—those that produce fertile pollen and eggs, and those that produce fertile eggs but sterile pollen. Very few, if any, varieties are com-

pletely sterile except under extreme conditions. Varieties that produce fertile pollen are self-fertile and may be used to produce selfed seed, or they may be used to pollinate varieties that have sterile pollen, thus giving cross-bred seed. In general, varieties that produce an abundance of fertile pollen are called males and those that produce little or no fertile pollen are called females.

The fertility or sterility of the pollen is not always a constant characteristic of a variety. Varieties which have fertile pollen in one locality may have sterile pollen in another, and some varieties change from year to year depending on weather conditions preceding and during flowering. Other varieties are rather constant in their behavior. In addition, there are a few varieties that produce fertile pollen but are apparently self-sterile.

The Technique Used in Crossing

At the present time emasculation¹⁰ of the flowers of one variety before pollinating is not practiced. The method was used to some extent in Barbados, Java, and Queensland, but the skill required, the uncertainty of the results, and the small number of seedlings obtained have prevented its extended use. The general practice now is to use the entire inflorescence as a unit. In making a cross between varieties or species, the female chosen is always one that has sterile pollen. Thus there is no possibility that this plant can fertilize itself. Since the entire inflorescence is used as a unit, the technique of crossing two varieties is rather simple. The female variety is grown in or moved to an isolated place so that chance cross-pollination is avoided. The male tassels are cut with several mature joints of stalk and are bound to the female tassel in such a way that the flowering parts of the female are covered by two or more male tassels. The tassels are not covered by bags. Pollination is continued for 6 to 10 days.

In Java, where successful cane breeding has been carried on for 50 years, the cut end of the stalk of the male tassel is placed in a jar of water. Since the tassels remain viable in water for 1 or 2 days at the most, they are renewed daily during pollination. The female inflorescences or "arrows" are left attached to the parent plants in the field. After pollination, the female tassel remains in the field until the seed is mature. This method is known as the open-cross method.

The method used in India is quite different. A large number of stalks of varieties in the early flowering stage are rooted by fastening a container filled with earth and kept moist to the middle of the stalk. In a short time the canes form a good root system in the pots. When flowering begins, the cane is severed below the pot and transported to a protected place. Crosses are made by bringing the desired male and female varieties together. Since each stock is rooted in a pot, it can be kept alive until pollination is completed and the seed matures.

While the Javanese and Indian methods are very successful, they both involve a great deal of labor and are adapted only to countries where labor is cheap. The Javanese method also requires a large number of male tassels.

Breeding stations in countries where wages are high and station budgets are limited have in general adopted the Hawaiian sulphurous-acid method of preserving the tassels (13, 19). This method is a major contribution to the technique of sugarcane breeding. When

¹⁰ Removal of the stamens, the organ that bears the pollen or male germ cells.

in the proper stage of development for crossing, the male and female tassels are cut with several feet of stalk attached and placed in a vessel containing a solution of 0.01 percent of sulphurous acid and 0.01 percent of phosphoric acid. The vessels containing each cross are isolated and left until the seed matures, which usually takes from 20 to 30 days. Fresh solution is added daily to replace the solution taken up by the stalks, and every week the solution is renewed. When the method is used in open crosses, the female is left growing in the field and the male tassels are preserved in the solution.

Most varieties keep very well in this solution, and the few that do not, if female varieties, can be left in the field or planted in isolated places; if male varieties, the tassels can be renewed when necessary. By this method it is possible to carry on an extensive breeding program with a minimum of labor.

The capricious nature of the sugarcane plant with regard to flowering makes it very difficult to carry on a definite breeding program. The only definite thing about flowering is that it is seasonal and seldom occurs outside the Tropics. The flowering season in the Northern Hemisphere is during the winter months and in the Southern Hemisphere during the short-day period which corresponds to our summer months. Some varieties have never been known to flower. Some flower nearly every season, but during a particular season may not flower at all, or only sparsely. Others may flower only once in 5 or 6 years. Certain crosses may not be possible because the two varieties flower at different times or because both are of the same sex.

The one great advantage the sugarcane breeder enjoys is vegetative propagation. Once a variety is obtained, it can be increased and perpetuated true to type by cuttings. It is not necessary to purify the type so that it will come true, as is the case with plants propagated from seed.

The methods of breeding vary somewhat from station to station. However, they have many points in common so that a review of methods and results at a few stations in different parts of the world will show the essential features of the improvement of sugarcane by hybridization. The world sugarcane-breeding stations are listed in tables 4 and 5 with their past, present, and projected work, personnel, and expenditures. Much of the information from which the material in tables 4 and 5 was assembled was derived from answers to a questionnaire sent to sugarcane breeding stations. In a few instances the replies arrived too late to be included.

BREEDING WORK AT THE JAVA STATION (1886)

The Java sugarcane-breeding station is notable for two lines of crosses—those between *S. officinarum* × *S. barberi* and *S. officinarum* × *S. spontaneum* (14).

Kobus crossed Black Cheribon, the chief sugarcane then cultivated in Java, with Chunnee, a variety from British India. His object was to obtain hybrids with a high sugar content, the size of Black Cheribon, and the vigor and sereh resistance of Chunnee. The seedlings were immune to sereh, but the sugar production did not equal that of the noble parent. In addition, they were susceptible to mosaic, though rather tolerant of the disease. Great success was attained, however, with the cross of the noble varieties Black Cheribon and Gestreept Praenger × Chunnee. Seedlings from these crosses,

P. O. J. 213,¹¹ P. O. J. 234, P. O. J. 36, and P. O. J. 36-M, were extensively cultivated in Louisiana, Argentina, Taiwan, and British India.

Later, Kobus crossed the F₁ or first hybrid generation seedlings with different noble varieties and obtained progeny with larger stalks and higher sugar content. But these varieties were not very hardy and none of them was as commercially successful as the F₁ seedlings.

Moquette and Wakker crossed Black Cheribon with Kassoer. They assumed that Kassoer was a wild cane, a botanical species of sugarcane. It has since been shown that Kassoer is a natural hybrid of *S. officinarum*, most probably Black Cheribon, and *S. spontaneum* of Java. The purpose was to obtain varieties with a higher sugar yield

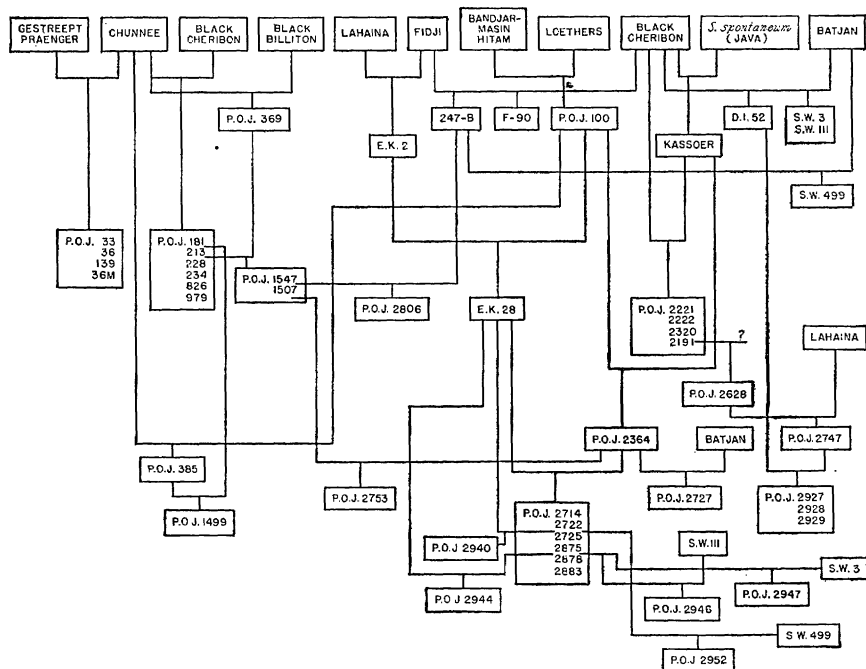


FIGURE 12.—Parentage of Java (P. O. J., Proefstation Oost Java) hybrid sugarcane.

and greater resistance to disease. The seedlings, however, were very disappointing in habit of growth and sugar content, and all of them were discarded.

During this time (1886-1911) commercial varieties were produced by crossing noble varieties. The outstanding noble hybrids were P. O. J. 100, 247-B, D. I. 52, E. K. 2, and E. K. 28. These hybrids were not only of commercial value but also important parents in the subsequent breeding program.

¹¹ Many varieties of sugarcane bred at experiment stations are designated by letters or other abbreviations, usually indicating the place or institution where they originated. The meanings of such designations for varieties mentioned in this article are as follows: P. O. J.=Proefstation Oost Java; Co.=Coimbatore (India); C. P.=Canal Point (Fla.); E. K.=Edward Karthaus, S. W.=Serpul Wadak; D. I.=Dimak Idjoe; C. P.=Saint Croix; B.=Barbados; Ba.=Barbados selfed; B. H.=Barbados hybrid; D.=Demerara; H.=Hawaii; M.=Mauritius; R.=Reunion; F. C.=Fajardo Central; P. S. A.=Philippine Sugar Association; S. J.=South Johnston; Q.=Queensland.

In 1910 Wilbrink crossed the noble varieties, Gestrept Praenger, Black Cheribon, and P. O. J. 100, with Kassoer. The progenies were not of commercial value, but they furnished the breeding stock which was used by Jeswiet to produce the very high yielding, disease-resistant varieties, P. O. J. 2714, P. O. J. 2725, P. O. J. 2878, etc.

The important step in the production of these varieties was the back-crossing to noble varieties. This process has been called nobilization. Thus, if Kassoer is a hybrid of *S. officinarum* (a noble cane) \times *S. spontaneum*, it is a seedling of the first nobilization. The cross of the F_1 , or Kassoer in this case, to a noble cane (P. O. J. 100 \times Kassoer) gives seedlings of the second nobilization, P. O. J. 2364. The cross of the seedlings of the second nobilization to a noble cane (P. O. J. 2364 \times E. K. 28) gives seedlings of the third nobilization, P. O. J. 2725, P. O. J. 2878.

The parentage of the important hybrids is given in figure 12.

The diagram shows that the noble parents were for the most part varieties formerly of high commercial value—Black Cheribon, P. O. J. 100, E. K. 28, D. I. 52, S. W. 3, S. W. 111, S. W. 499. The other parents, Kassoer and P. O. J. 2364, have good agronomic characteristics, but they are of no direct commercial value because of their low yields of sugar. It appears, therefore, that varieties which prove to be of value as parents possess themselves some qualities which distinguish them from the bulk of the varieties.

It is also important to note that while the breeding program is essentially a nobilization of Kassoer, the supposed original parent, Black Cheribon, is not used, but the dilution of *S. spontaneum* blood is by means of crosses to other noble varieties. Thus the crosses are back crosses only in a very broad sense.

This method of breeding has produced several commercial varieties. Unquestionably, P. O. J. 2878 is the most important. It is immune or resistant to the major sugarcane diseases, and its yield of sugar per unit area is much greater than that of any variety ever grown in Java. Although it is a commercial cane in other countries, it is preeminently adapted to the country for which it was produced.

BREEDING WORK AT THE BARBADOS STATION (1887)

Sugarcane breeding was begun in Barbados almost simultaneously with the work in Java. Until recent years all the seedlings were from selfs or crosses of varieties of *S. officinarum* (12). This is the most extended breeding program within a single species of sugarcane. Prior to 1902 the parents were not known, and for the whole period, 1887–1925, seedlings were from chance-pollinated varieties, supplemented by seedlings from controlled pollination. The result of this program was the development of five distinct lines of noble varieties of different descent.

Two of the lines are descended from White Transparent. The original parent or parents of the other lines are not known, but it is very probable that these lines were derived from a very few noble varieties.

Varieties in each line have characteristics in common and are the nearest approach to “pure” lines obtained in sugarcane. Crosses

between varieties from different lines produce better seedling populations than crosses between varieties of the same line. Thus there is some indication at least that the lines are tending to become homozygous or pure for certain characters.

The seedlings obtained from these crosses are well suited to conditions in Barbados and a greater part of the West Indies. In general, the varieties are excellent from the standpoint of milling and juice quality, because the fiber content is low and the percentage of sucrose in the juice is high. The relatively infrequent flowering is a highly advantageous feature under conditions where considerable vegetative growth may still be made during and after the flowering season if the plants have not flowered. The varieties yield a relatively good tonnage of cane on a wide range of soil types and are easily cut and transported. They have produced types which yield rather well under an annual rainfall of slightly less than 40 inches.

These varieties have several defects. Germination and establishment of a crop is not as good as with the Javanese and Indian varieties. They are susceptible to drying and rotting after being cut. The canes on aging offer little resistance to the attack of weak parasitic or saprophytic fungi. They are all susceptible to mosaic, which limits the area in which they can be planted.

The most important seedlings produced in Barbados are B. H. 10/12 and S. C. 12/4, but many other seedlings have been and are grown commercially.

When it is considered that only a few noble varieties were used to produce these excellent seedlings, and that other stations have produced highly productive varieties from a few noble parents, it is evident that the full amplitude of variation of *S. officinarum* has not been utilized. A wide range of crosses within the species might produce additional commercial varieties and without a doubt would produce valuable breeding material.

At the present time the Barbados station is crossing Barbados varieties with outstanding noble varieties produced at other stations, and is also using these varieties in interspecific crosses in a nobilization-breeding program similar to that employed in Java.

BREEDING WORK AT THE COIMBATORE STATION (1912)

In British India sugarcane is grown over a large area where soil and climatic conditions are not favorable for varieties of *S. officinarum*. The hardy indigenous varieties are adapted to these conditions, but their yield of sugar is very low. The problem of the breeder at Coimbatore, India, is to produce high-yielding varieties adapted to these conditions (17).

During the first few years of breeding at Coimbatore a Javanese variety, P. O. J. 213, was largely used as a female parent. It had to be given up, however, because of the susceptibility of its seedlings to mosaic, red rot, and smut. In recent years most of the parents employed are of Coimbatore origin.

Coimbatore was the first station to deliberately use *S. spontaneum* (India) in crosses with *S. officinarum* (1912). It is remarkable that a commercial seedling, Co. 205, was obtained from the first generation.

Co. 205 (18) has a fair sugar yield and is susceptible to mosaic. Its behavior is in marked contrast to the behavior of the F_1 seedlings of *S. officinarum* \times *S. spontaneum* (Java), which have a low sugar content and are immune to mosaic.

The parentage of the Coimbatore seedlings and the essential features of the breeding program are shown in figure 13.

Several of the important seedlings, Co. 281, Co. 290, Co. 221, are hybrids of three species of sugarcane, *S. officinarum*, *S. spontaneum*, and *S. barberi*. These trihybrid varieties are particularly well adapted to culture in subtropical regions. They are commercial canes in India, Australia, Louisiana, Natal, Argentina, Brazil, and on the poorer soils of the Tropics.

The Coimbatore station is also breeding canes for the tropical portions of India. In this program noble varieties, Coimbatore hybrids, Kassoer, and Javanese hybrids are the type of parents used. It is essentially a nobilization program, the purpose of which is to produce thick-stalked varieties especially adapted to tropical India.

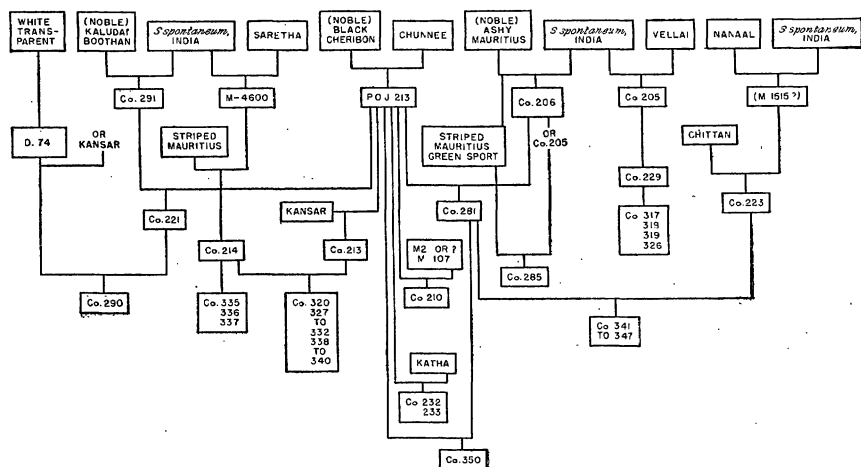


FIGURE 13.—Parentage of Coimbatore sugarcane seedlings. Many of the parents are putative.

BREEDING WORK AT THE CANAL POINT STATION (1918)

Canal Point, Fla., is one of the few places outside the Tropics where sugarcane flowers. While the number of varieties that flower is not so great as in the more favorably located tropical stations, it is sufficient for carrying on a rather extensive breeding program.

During the first 10 years the breeding work was dominated by economic considerations and the need to produce quickly a new cane to replace the old noble varieties D-74 and Louisiana Purple, which had failed largely because they were susceptible to mosaic, root rot, and red rot (fig. 14). During this period the station produced C. P. 807, C. P. 28/11, and C. P. 28/19, disease-resistant varieties adapted to the soil and climate of the sugarcane areas of the United States. These three varieties and two importations, Co. 281 and Co. 290, are now



FIGURE 14.

Resistance to mosaic by breeding: *A*. The two middle rows are of a variety formerly grown in Louisiana but completely eliminated because of extreme injury by mosaic. The two end rows at the left are of a variety obtained by crossing the variety in the middle rows with a variety from India somewhat resistant to mosaic. The two end rows at the right represent results of crossing the hybrid thus obtained with another hybrid having one-half of the blood of the wild cane *Saccharum spontaneum*, which is immune to mosaic.

the standard canes, and under field conditions they have proved a great advance on the old varieties formerly cultivated.

All of these varieties were products of a hit-or-miss method, which is the common method at all sugarcane-breeding stations. Beginning with 1928, however, a definite system of crosses was initiated with the purpose of building up breeding stocks of known constitution. Essentially, this is a program of crossing, back-crossing, and selfing, accompanied by selection, in an effort to improve varieties of sugarcane without interfering with their behavior in hybrid combination. The plan is intended to accomplish this by combining the favorable factors from two or more varieties into a single variety. Figures 6-10, previously noted, illustrate this process.

The success of the program depends upon the selection of parents of proven value. By evaluating the progenies produced in former years, it was possible to select four combinations which gave seedlings approaching the desired type. Following the selection of parents, the essential steps in the breeding program are:

(1) Two varieties, *A* and *B*, possessing the desirable agronomic characters—some characters in *A* and some in *B*—are crossed.

(2) Selected F_1 seedlings are back-crossed to one parent *A*, to recover or intensify the important characters of that variety. Seedlings retained from this cross are those that have the essential factors from *B*, which was not used in the back-cross.

(3) At the same time the best pollen-fertile seedlings are used to start selfed lines, from which the individuals that approach the desired type are selected. This inbreeding is an attempt to fix the added characters so that they will breed true.



FIGURE 14.

* B, Comparative yields obtained from the three varieties illustrated in A. Mosaic was rampant in this field when the picture was taken.

(4) These operations are performed with each of the original varieties as the parent used for back-crossing. It is important to note, however, that the same F_1 seedling cannot be back-crossed to both parents, because emasculation of the parent with fertile pollen (the male) is not practicable. Therefore, selected male F_1 seedlings are back-crossed to the female parent and selected female F_1 seedlings are back-crossed to the male parent.

(5) Further improvement will be obtained by repeating the operations, using the recovered varieties (selected seedlings from the third or fourth back-cross) in place of the original varieties as foundation stock and introducing new factors by crossing recovered varieties from other lines.

The method is slow, since it takes 5 or 6 years to make four or five back-crosses, yet it affords the same opportunities for the production of new commercial varieties as a system based on chance alone, and at the same time it furnishes a means of building up breeding stock of known potentialities.

Since parents used in the breeding program are species hybrids, the behavior of the chromosomes with respect to deviation in number (see section on chromosome behavior p. 597) will have an important bearing on the result. Fortunately, the commercial propagation of sugarcane is by cuttings; therefore, any useful variety produced by chromosomal aberration may be readily propagated and exploited.

The review of the work at the stations in Java, Barbados, India, and Florida gives a general idea of the methods used in breeding new varieties of sugarcane. The breeding at other stations does not differ in any essential feature. Summing up briefly, the most impor-

tant results have been obtained from (1) crosses of *S. officinarum* × *S. spontaneum* and subsequent nobilizations; (2) the crosses of *S. officinarum*, *S. spontaneum*, and *S. barberi*; and (3) varietal crosses within the species *S. officinarum*. While important seedlings have been produced by crosses between varieties of the same species, the crosses between species are of much greater economic importance. These crosses have produced disease-resistant varieties that have increased the yield per unit area by several fold and are adapted to a wide range of soils and climatic conditions.

It is important to note that the brilliant achievements of the past are the result of methods that depended largely on chance. This is not due entirely to lack of a breeding program, but rather to the capricious nature of the sugarcane plant, which makes it very difficult to follow a definite plan.

Aside from the production of improved commercial varieties, the trial-and-error method has produced a large amount of breeding material, so that it is now possible to carry on a program with a view to determining the inheritance of the more important characters. But until something more is known about the genetics of sugarcane, the best combinations will be found by a trial-and-error method in the hands of an intelligent and industrious breeder who makes a large number of crosses and observes the progenies under the particular conditions for which he is attempting to produce a new variety.

Crosses Between Sugarcane and Other Genera

Perhaps the most outstanding intergeneric hybrids among plant crops are those that have come from the maize-teosinte, wheat-rye, and sugarcane-sorghum crosses. Sugarcane has also been crossed with species of the closely related genus *Erianthus*. The crosses of *S. officinarum* with *Erianthus* have not produced any commercial types of canes (15). The F_1 seedlings resemble sugarcane more than they do *Erianthus*, but they definitely possess *Erianthus* characters. Most of these hybrids are pollen-sterile, but a few have from 10 to 30 percent of good pollen, so that it will be possible to carry on further breeding. At present very little is known of the commercial value of these interesting hybrids.

The cross of sugarcane-sorghum holds greater commercial promise. The purpose of the cross was to produce a variety of sugar plant that would mature in about 6 months. It would be especially valuable in the sub-Tropics, because such a variety would increase the number of working days in a factory, obviously a factor in lowering the cost of production. There is also the possibility of extending sugarcane production into the temperate zones.

The first sugarcane-sorghum cross was made by Thomas and Venkatraman (16) at Coimbatore, India. They crossed the sugarcane P. O. J. 2725 and *Sorghum durra*, Stapf, a grain sorghum. This cross has been repeated at the United States Sugar Plant Field Station, Canal Point, Fla., and in addition several crosses have been made between P. O. J. 2725 and other sugarcane varieties and varieties of sorgho.¹² The hybrids include many albinos, which die in the seedling stage. Of the remainder, a large number are abnormal and develop into obviously uneconomical types. Fortunately, there are quite a number of hybrids that grow like sugarcane and have a good sugar content. Thus far, however, early maturing commercial types have

¹² Sorgho=sweet sorghum.

not been produced. The progress made in a few years is encouraging, and hybridization of sugarcane with other genera seems to be justified. It will require several years of breeding to determine the practical possibilities of this method.

The Slow Process of Progeny Testing

The possibility of crossing different species and genera is most attractive to plant breeders and agronomists, since by this means the most useful characters of two or more species may be combined in a single variety. Most plant breeders have been skeptical of applying the method, especially to plants reproduced by seed. The results with sugarcane, which is vegetatively propagated, lead to greater optimism, since there were no outstanding disease-resistant varieties produced until species crosses were resorted to. Practically nothing, however, is known about the inheritance of characters in the highly polyploid species of *Saccharum*.¹³ An added difficulty is that the majority of economically significant characters are quantitative. In the past, quantitative characters have been neglected because of their complicated nature and the existence of so many intermediate forms. Even for simple diploid plants, about which most is known genetically, there are only fragmentary data on the inheritance of quantitative characters. In dealing with such a complex problem, the scale on which the work is carried out is of extreme importance. In order to find valuable forms combining the useful characters of the parents, it is essential to produce large progenies for several generations.

It is evident that for successful breeding of heterozygous polyploid plants, it is necessary to have a method for the accurate determination of the breeding value of parent varieties. The progeny test, which consists essentially in determining the number and proportion of the various kinds of seedlings produced by an individual or cross, provides the most reliable method of evaluating the breeding potentialities of the parents.

This method is used at Canal Point to determine the breeding value of the parents in the different crosses. Large progenies of the best crosses are sent to the major sugarcane districts of the United States and tested for their adaptability to the conditions in each district. It is essential that the progeny test be conducted under the environmental conditions in which the variety presumably will be grown, so that they may be subjected to the disease, soil, and climatic factors that will determine the success or failure of the new production.

The essential features of the method used for testing the progeny and selecting new varieties, which is long and painstaking, will be outlined briefly.

Two varieties that possess the essential characters between them are crossed, and if the resulting individuals approach the desired types, they and subsequent progenies are sent to the district for which the new variety is intended. Finding a productive combination may take from 1 to several years. Let us suppose that the progeny is to be tested in Louisiana. It is necessary to segregate those varieties that are adapted to the soil and climatic conditions of Louisiana. The individuals selected must be vigorous and early maturing, have

¹³ See the later section on chromosome behavior, p. 597.

good keeping qualities in the windrow, and be resistant or immune to mosaic and red rot.

During the first year every individual of the progeny is inoculated with mosaic. This is done because under natural conditions the disease fluctuates between wide limits in its spread, and a susceptible variety may escape infection for several years. If the plants are artificially inoculated, it is possible to segregate the susceptible and immune varieties during the first year.

Beginning early in the autumn, the sucrose content of all the individuals that approach commercial types is determined. Those that have a satisfactory sugar content and early maturity are segregated from the rest. These seedlings are now inoculated with different strains of red rot (*Colletotrichum falcatum*), and only those that are resistant to the extent required commercially are retained and planted in increase plots on different soil types.

The next year the seedlings are given the same treatment, and the original planting is observed to determine the stubbling qualities of the selected individuals. The varieties that continue to show promise are sent to various places throughout the State to be increased; or, if the supply of cuttings is ample, they are planted in replicated variety tests.

In these tests the yielding capacity of the new variety is compared with that of the standard commercial varieties for at least 3 years. If the new variety is superior, it is released for commercial culture. It usually takes from 5 to 6 years to test a new variety. Before it is released, it is necessary to determine the yielding capacity per unit area, resistance to the major diseases, and the soil type to which it is best adapted. The data collected are a further contribution to our knowledge of the inherent characteristics of the parents.

The improvement of varieties by hybridization and progeny testing has many ramifications. It is a vast field in which the efforts of the agronomist, cytologist, plant pathologist, and plant breeder are combined.

Theoretical and Practical Progress Go Hand in Hand

Throughout the long history of sugarcane culture there has been a continuous procession of varieties. A variety attained commercial prominence and was successful for a varying period of years. Owing to a change in conditions, diminishing soil fertility, or the incidence of disease, the variety failed. It was then replaced by a new and superior variety. There seems to be no end to this process. The ideal sugarcane, with its characteristics, is but vaguely formulated and reformed after each advance. It must be remembered that the sugarcane plant is a living, dynamic thing that can be molded into an almost infinite number of forms. Each advance, trivial though it may be in relation to the ultimate goal, is a reward and an incentive to continued endeavor.

From the theoretical standpoint, our knowledge of *Saccharum* is very fragmentary. It is essential for further improvement that a world collection of all the cultivated and wild species of sugarcane and closely related grasses be made. For more than 15 years the United States Department of Agriculture has been assembling cultivated and wild varieties of sugarcane from all over the world. Emphasis is placed on the areas where the plant is presumed to be

indigenous, and collections have been made in southeastern Asia and islands of the Pacific, including Taiwan, the Philippines, New Guinea, the New Hebrides, New Caledonia, and the Loyalty, Fiji, Tonga, Samoa, Cook, Hawaiian, and Society Islands.

The area is vast, communication is difficult, and progress is slow, but in four expeditions during the 15 years several hundred varieties have been collected and more than half of them have been safely established in the United States. The material that is now available and that which will be obtained will make it possible to place the whole problem on a new footing. Then by breeding within the species, choosing the extreme types as parents, it will be possible to determine the full amplitude of natural variation within a species and the potentialities for developing new and useful types by species hybridization.

It may appear that all the above is purely theoretical. The important and remarkable feature of modern plant breeding, however, is that the solution of the main theoretical problems is simultaneously leading to the solution of the most urgent problems of practical agriculture.

Chromosome Numbers and Chromosome Behavior in the Sugarcane

WITH few exceptions, the number of chromosomes in the cells of an individual is constant and characteristic of the species to which the individual belongs. Different species may have the same number of chromosomes, but it is needless to point out that they are qualitatively very different. The chromosomes themselves possess a definite individuality. Therefore, the chromosome numbers may be of value in determining whether or not a classification based on morphological character, or form, is correct. They also may offer evidence in efforts to trace the probable ancestors of sugarcane.

Before taking up these questions it may be well to review briefly the normal behavior of the chromosomes in sugarcane. It has been pointed out above that the number of chromosomes in the cells of an individual is constant and characteristic of the species to which it belongs. For example, the varieties of *Saccharum officinarum* have 80 chromosomes in their cells. It is not necessary here to show how this number is kept constant during the growth of the plant by cell division, but merely to state that when a cell is about to divide the chromosomes split lengthwise into two parts that are quantitatively and qualitatively equal, thus forming pairs of chromosomes. The chromosomes of each pair separate from each other, moving to opposite poles of the cell, and a cell wall is formed between the two groups. The division of the cell gives rise to two daughter cells, each of which contains exactly the same number of identical chromosomes. This number is called the somatic, diploid, or $2n$ number of chromosomes. When sexual cells are formed, a different set of phenomena occur which results in the reduction of the number of chromosomes to one-half of that characteristic of the somatic or body cells. This is

accomplished by what is known as the reduction division. In this division the chromosomes do not split longitudinally, but each chromosome derived from the male parent pairs or associates homologously throughout its length with its homologue, the like chromosome derived from the female parent. Thus if there were 80 chromosomes to start with, there are now, at the time of the division, 40 double or paired or bivalent chromosomes. The members of each pair then separate and are distributed to opposite poles of the cell. When the cell itself divides, each of the two daughter cells receives one member of each pair of chromosomes, or 40 chromosomes in all. In this way the sexual cells (eggs and pollen) of noble canes receive 40 chromosomes. In the reduction division the segregation of one pair

LACK of resistance to mosaic in varieties of sugar-cane formerly grown in Louisiana brought the industry to the brink of ruin a dozen years ago. Production of sugar fell from an average of over 200,000 tons to a low of 47,000 tons a year, and it is estimated that losses to the sugar and sirup industries of the South amounted to \$100,000,000. Plant breeders began a world-wide search for resistant varieties and instituted a program of selection and breeding. Results have exceeded expectations. After being forsaken as a business risk by almost all financing institutions, the sugar industry in the South has been restored, and yields per acre are now higher and are obtained at less cost than before the mosaic epidemic. The plant breeder has demonstrated that he can not only meet the challenge of diseases, but turn it to advantage.

of chromosomes is entirely independent of that of any other pair, so that there can be as many different combinations as chance might bring about among 40 different pairs. The reduced number of chromosomes is known as the monoploid (haploid) or n number of chromosomes.

Now when an egg that has 40 chromosomes is fertilized by a sperm bearing 40 chromosomes, the resulting zygote will develop into a plant with 80 somatic chromosomes. This number, as we have seen, is a constant characteristic of *S. officinarum*.

The study of chromosome number has revealed a phenomenon that occurs rather frequently in plants. It is often found that the number of chromosomes of the species of a genus is a multiple of a constant

or basic number. In wheat (*Triticum*) the basic number is 7, and there are species with 14, 28, and 42 chromosomes. Thus, there are species with two, four, and six sets of 7 chromosomes, and these species are respectively diploid, tetraploid, and hexaploid. In sugarcane the basic number is probably 10, but whether it is a primary or secondary basic number is an open question. The species of *S. officinarum* have, on this assumption, 8 sets of 10 chromosomes. The plant, therefore, is octoploid. All the known species of sugarcane are polyploids, that is, they have several sets of the basic number. The simple diploid forms with 20 somatic chromosomes are unknown.

In diploid plants which have two sets of homologous chromosomes, the segregation of characters follows along rather simple Mendelian lines. In tetraploid and higher polyploid plants, the segregation becomes much more complicated so that it is very difficult to work out the mode of inheritance of a character. Thus, in sugarcane, which is octoploid, if on hybridization the chromosomes of any one set are capable of pairing with their respective homologues of any of the seven other sets, the possible number of different chromosome combinations will be so enormous that a representative progeny could not be raised in a lifetime.

Since all the species of sugarcane are polyploid, the exact nature and segregation of hereditary factors may never be worked out. In addition, all sugarcanes are heterozygous to a high degree, and all individuals resulting from varietal or species crosses are heterozygous. There is, however, considerable knowledge of the behavior of the chromosomes of different lines of descent in hybrid combination.

SEARCHING THE CELLS FOR EVIDENCE OF ANCESTRY

The distribution of the wild forms of sugarcane is partially correlated with chromosome number. In general, the forms with the higher number of chromosomes are confined to the Tropics and the forms with a lower chromosome number extend into the subtropical and temperate zones. Thus, the forms with 112 and 124 somatic chromosomes are found in Java and the islands nearby. The forms with 80 somatic chromosomes extend northward to the Philippines and Taiwan. Intermediate forms with 96 chromosomes are found in the Celebes and Indochina. In British India are forms with 78 and 64 somatic chromosomes. There are exceptions; the Tananggé of North Celebes with 60 somatic chromosomes and *S. robustum* of New Guinea with 82 somatic chromosomes, so far as is known, are confined to the Tropics.

A fact that may be significant, however, is that in British India there are distinct forms of *S. spontaneum* and also distinct groups of cultivated canes that differ remarkably from the cultivated canes of the Tropics. The forms of *S. officinarum* attain their maximum growth in the more essentially tropical areas, while the forms peculiar to British India are adapted to a cooler climate and do not succeed in the Tropics. It appears, therefore, that the cultivated species of sugarcane originated in different places and presumably from different lines of descent.

The chromosome numbers of the existing forms do not give any clues to the descent of the cultivated species. The basic number of *Saccharum* is probably 10. Diploid forms of *Saccharum* with 20

somatic chromosomes, forms that could be considered primitive, are not known. This also applies to the tetraploid forms with 40 somatic chromosomes. They probably are extinct, but it is possible that they may still exist. The simplest forms known are the Tananggé cane of the Celebes, a hexaploid with 60 somatic chromosomes, and the octoploid forms of *S. officinarum* and *S. spontaneum* Tabongo. Most of the other known forms of *Saccharum* have chromosome numbers that are not a multiple of 10, but are aneuploids. Thus, the British Indian canes have 82, 91, 107, 116, 124. Forms of *S. spontaneum* have 64, 78, 96, 112, 124. *S. robustum* has 84 chromosomes. All the known

THROUGHOUT the long history of sugarcane culture there has been a continuous procession of varieties. A variety attained commercial prominence, was successful for a few years, then failed because of changed conditions, diminishing soil fertility, or disease—to be replaced by something new and superior. There seems to be no end to this process. It must be remembered that the sugarcane plant is a living, dynamic thing that can be molded into an almost infinite number of forms. It is essential for further improvement that a world collection be made of all cultivated and wild species and closely related grasses. For more than 15 years the Department of Agriculture has been making such a collection. With such material available, the problem is placed on a new footing, since it will be possible to determine the full range of natural variation within a species and the possibilities for developing useful new types by hybridization.

species of *Saccharum* are complex polyploids or aneuploids. Chromosome balance is very important in developing new species.

The main course of evolution appears to have proceeded by changes in the number and qualities of the chromosomes, natural selection preserving the changes that have a positive survival value. With the passage of time a given species may acquire a different genetic constitution, owing to the accumulation of mutations. By this means variation within a species may give rise to specific forms which, when crossed, give only sterile hybrids because of the differentiation of the chromosome sets and consequent failure of pairing in the hybrid. Thus species which have descended from a common ancestor and still

have many characters in common will produce sterile hybrids because the chromosomes are too different to pair.

These hybrids can survive sexually if doubling of the chromosome number occurs, for then each chromosome has an identical mate. The chromosomes pair normally and fertile germ cells are formed.

In the genus *Saccharum* there are several species and many varieties, all of which give fertile hybrids. In most of the species crosses there is a doubling of the chromosome number of one parent. So long as it does not disturb the normal proportion of elements, a change in the number of chromosomes—as in the hybrids of *S. officinarum* × *S. spontaneum* where the entire set of the noble chromosomes is doubled—does not greatly alter morphological characteristics, but does tend to increase size and yielding capacity with ascending multiples of the monoploid number. While doubling of chromosomes in the hybrids of diploid plants produces distinct types, it appears that the highly polyploid forms of sugarcane are probably of little importance in the evolution of new forms or species.

Changes that disturb the chromosome balance, however, are of primary importance in evolution. For instance, the loss of a single chromosome, leaving some specific chromosome without a homologue, disturbs the genetic balance in its entirety. This alters the inter-relationship of the chromosomes, and the factor balance previously associated with the normal phenotype, and thus produces a general morphological change. The loss of a single chromosome usually causes a greater morphological change than the duplication of an entire set.

It is quite apparent that in highly polyploid plants like sugarcane, which have several sets of homologous chromosomes, a slight change in chromosome number probably would not disturb the balance or produce an appreciable morphological change.

It seems very improbable that the cultivated forms of *S. officinarum* could have originated from hybridization between species of the existing complex wild forms, followed by a doubling of the chromosome number, because the cultivated species have a rather low chromosome number comparatively speaking. The large difference in chromosome number makes it just as improbable that they could have arisen through chromosome aberration, either by the elimination of chromosomes in the somatic division or by the formation of aberrant gametes.

The doubling of the chromosomes of *S. officinarum* in crosses with the other species of *Saccharum* indicates a different line of descent. Since most of the other possible species crosses have not been studied, the chromosome behavior is not known, except for the cross of a British Indian variety, Saretha × *S. spontaneum* Coimbatore. In this cross there was no doubling of chromosomes, which may indicate a relationship between the Indian cultivated varieties and the Indian forms of *S. spontaneum*. Even in this case, however, the chromosomes from the different species may have paired among themselves.

The incidence of mosaic disease in the species and species crosses gives information that may be of value in tracing descent. All the species of *S. spontaneum* except *S. spontaneum* Koelawi A are immune, while all the varieties of *S. officinarum* and all the cultivated forms of British India are susceptible. The hybrids of *S. officinarum* and the forms of *S. spontaneum* with 112 and 80 somatic chromosomes are immune, while hybrids of noble varieties and *S. spontaneum* forms of

India are susceptible. It seems from this point of view that the Indian cultivated canes are more closely related to the Indian *spontaneum* than the noble canes are to the tropical varieties of *S. spontaneum*. The only other known wild species, *S. robustum*, is susceptible to mosaic. Some of its morphological characters are similar to those of *S. officinarum*, and the behavior of the chromosomes of these species in hybrid combination indicates that many of their chromosomes may be homologous. It appears, therefore, that *S. officinarum* and *S. robustum* are rather closely related and probably are from the same line of descent.

Experimental breeding with sugarcane species and closely related grasses may shed more light on the origin of the cultivated sugarcanes. For the present it seems that the most plausible theory of the origin of the cultivated species is that besides *S. spontaneum* and *S. robustum*, other species of *Saccharum*, which are unknown or perhaps extinct, have also contributed to the formation of these species.

THE RELATION OF CHROMOSOME NUMBERS TO BOTANICAL CLASSIFICATION

The chromosome numbers of the species of *Saccharum* as at present classified, and of two closely related genera of grasses, are given in table 2.

TABLE 2.—*Diploid chromosome number of species of Saccharum and related grasses*¹

Species	Group ²	Variety	Chromosome Number
<i>S. officinarum</i>		Creole ³	80
		Loethers	81
		P. O. J. 100	98-99
		Uba Marot	88-90
		Naz Reunion	113
		Kara Kara Wa	109-110
			124-126
<i>S. sinense</i>			118
	Pansahi	Kavangire	118
		Uba	116-118
		Cayana	116-118
<i>S. barberi</i>	Sunnabile		116
		Dhaultu	82
	Mungo		82
	Nagori		124
	Saretha		90-92
<i>S. spontaneum</i>	Paseroean and other forms of Java, Sumatra, and Borneo.		112
	Tabongo, Paloe, Talahib of northern and central Celebes and the Philippines, respectively.		80
	Biroh of central Celebes and forms from Mandalay, Burma.		96
	Tananggé of northern Celebes and Teboe Salah of Borneo.	Glagah Krakatau	124
			60
	Coimbatore and Kellegaddi, India.	Sumatra (thin-stemmed)	108
		Sumatra (thick-stemmed)	128
		Dacca, India	64
		Dehra dun, India	78
<i>S. robustum</i>			54
<i>S. biflorum</i>			84
<i>S. narenga</i>			112
<i>Erianthus arundinaceus</i>			30
			60
<i>E. sara</i>		Coimbatore form	40
<i>E. elegans</i>			60
<i>E. ravennae</i>			40
<i>Sorghum</i>			20
<i>Miscanthus japonicus</i>			20
			38

¹ The chromosome counts are for the most part by G. Bremer.

² The groups are for convenience and do not necessarily represent botanical classifications.

³ The varieties here listed under *S. officinarum* are examples of the numerous varieties assigned to that species because of morphological resemblance but with chromosome numbers that depart from the number 40 usually found. Probably they are hybrids.

In the morphological classification of the species there are sufficient distinguishing characteristics between *S. officinarum* and *S. spontaneum*, but there seems to be a lack of good criteria on which to base the separation of *S. sinense* and *S. barberi*, though they are different enough in appearance and cultural characteristics.

Investigations of the chromosome numbers show that *S. officinarum* is a species the varieties of which form a homologous group (5). Study of many noble varieties shows that the somatic chromosome number of the group is 80. There are a few varieties, however—Loethers, Creole, Naz Reunion, etc.—that differ somewhat in morphological characters and chromosome number. These forms probably are hybrids between noble varieties and some unknown variety, and as a result of repeated back-crossing to noble canes they have retained only a few of the characters of the nonrecurrent parents.

There is a large number of varieties in *S. sinense*, but the chromosome numbers of only a few have been determined. All that can be said about them at present is that they seem to form a homologous group difficult to define, and that the somatic chromosome number of the few varieties that have been investigated is about 116–118.

Barber (2, 3) has made the most detailed studies of the indigenous sugarcanes of British India. He divided them, according to their external characters, into five groups—Sunnabile, Mungo, Nagori, Saretha, and Pansahi. Jeswiet identified the Pansahi group with *S. sinense*. In this group there are a number of varieties that do not occur exclusively in British India, but are found also in Indochina, South China, and Taiwan. The cane varieties that are native to British India belong to the first four groups, and these have been classified by Jeswiet under the name *S. barberi*.

With few exceptions the chromosome numbers corroborate Barber's classification (6, 7, 8). Each group has a distinctive chromosome number. The varieties of the Sunnabile group have 116–118 chromosomes. This number, however, does not occur in the Dhaulu subgroup, which Barber places under Sunnabile. On the other hand, the canes of the Dhaulu subgroup have the same chromosome number, 82, as the canes of the Mungo group. The Dhaulu varieties differ in a pronounced way from the canes in the Sunnabile group, though they also differ markedly from the varieties of the Mungo group. It seems desirable, therefore, to separate the Dhaulu varieties from the Sunnabile group and to make them a separate group closely related to the Mungo varieties.

It is remarkable that in the canes of the Nagori group, which resemble one another very much, there are two chromosome numbers, 124 and 107. Possibly the original number was 124 and the number 107 was derived from this by chromosome aberration or hybridization. This is merely an attractive supposition.

The chromosome numbers of the varieties of the Saretha group vary from 90 to 92. It might be possible that the forms having 91 chromosomes are hybrids between the forms having 90 and 92 chromosomes.

The list in table 2 includes only the British Indian varieties that have been investigated cytologically. A great many varieties are not represented. Some of these are varieties that Barber was not able to place in the present groups, and many are varieties that were classified but not available for cytological study. It must be remembered, too, that Barber divided the Saretha group and the Sun-

nabile group into two distinct sections according to the geographical distribution of the varieties. The earlier maturing and profusely branching forms occur near the Himalayas, while the late-maturing varieties are found in the peninsula.

From this brief review of the British Indian canes it is evident that grouping them under a species name, *S. barberi*, is rather arbitrary. Pending further investigation, it will be better to retain the separate groups of Barber.

Within the species *S. spontaneum* are forms that differ in external appearance and chromosome number. Table 2 shows that these forms have distinctive chromosome numbers, and that each form has a rather definite geographical distribution. In British India the form Dacca has 78, and the Coimbatore form has 64 somatic chromosomes. In the Philippine Islands, Taiwan, and northern and central Celebes are forms with 80 somatic chromosomes. The forms from Burma and central Celebes have 96 chromosomes. In north Celebes there is also the Tananggé cane with 60 somatic chromosomes. The forms of Java have 112 somatic chromosomes. This number is also found in many clones from Soembawa, Sumatra, and Borneo. A subspecies, *S. biflorum*, from north Africa, has the somatic number 112. The highest somatic chromosome number, 124, is found in a form from Krakatau, a group of small islands between Java and Sumatra. *S. robustum* from New Guinea, a wild cane which is distinct morphologically from the other wild forms, has 84 somatic chromosomes. A species called *S. narenga*, which may not be a sugarcane, has 30 somatic chromosomes.

This list does not include all the forms that would at present be placed in *S. spontaneum*. It is known that in British India there are at least seven different forms. Collections have only recently been made of wild forms in the Pacific islands to the east and southeast of Java. As knowledge concerning these wild canes increases, it probably will be possible to divide *S. spontaneum* into subspecies.

It may be of interest to note the chromosome numbers of genera closely related to sugarcane. In *Erianthus* there are species with 20, 40, and 60 somatic chromosomes. *Miscanthus japonica* has 38 somatic chromosomes.

The cytological investigations in the genus *Saccharum* are, as has been shown in the preceding paragraphs, an aid to classification. This, however, is merely incidental, because the essential function of the chromosomes is to furnish the mechanism for the distribution of hereditary characters.

BEHAVIOR OF CHROMOSOMES IN SPECIES AND GENERIC CROSSES

When a variety of *S. officinarum* with 40 monoploid chromosomes is crossed with a variety of *S. spontaneum* (Java) with 56, one would expect to find the somatic chromosome number of the F_1 progeny to be 96, the sum of the monoploid numbers of the parents. These individuals, however, have 136 somatic chromosomes. This number is exactly 40 more than the sum of the chromosomes in the sexual cells of the parents. The chromosomes of *S. officinarum* split longitudinally, thus doubling their number and forming pairs of homologous chromosomes, and those of *S. spontaneum* pair among themselves. Therefore the F_1 individuals have 80 noble and 56 wild chromosomes.

Since the chromosomes from the different lines of descent are able to pair among themselves, the reduction division of the F_1 individuals is regular, and generally speaking these individuals are highly fertile. Most of them produce fertile eggs and pollen, and only a few are pollen-sterile. Completely sterile individuals do not occur. This is rather unusual because as a rule species hybrids are sterile, and only occasional exceptions are fertile.

The character of the F_1 individuals is in general intermediate between that of the parents. But though the seedlings resemble one another, there is a good deal of individual variation. Since only the chromosomes of like descent will pair, one would expect the F_1 hybrid to breed true. In fact, the F_2 or second generation individual with few exceptions is very similar to the F_1 , and types resembling the parents never occur. Most of the F_2 plants have 136 somatic chromosomes, some have less than 136, and a very few may have one or two more than 136. This is due to the fact that the reduction division is not absolutely regular. There are usually from 4 to 12 chromosomes that do not pair. These univalent chromosomes are distributed at random so that sexual cells are formed with chromosome numbers which deviate slightly from the normal monoploid number, 68.

If now an F_1 is back-crossed to *S. officinarum*, the resulting hybrids will have 148 chromosomes. The sexual cells of the F_1 have 68 chromosomes, and the noble cane has 40. Therefore, the number of chromosomes expected would be 108. In this second nobilization there is again an increase of 40 chromosomes over the expected number. Apparently, these chromosome numbers arise because the chromosomes from the noble parent have doubled, so that the back-cross seedlings have received 80 chromosomes from the noble parent and 68 from the F_1 parent. Probably 40 of the chromosomes from the F_1 parent are noble and 28 are *spontaneum* (wild).

The individuals from this cross are immune to mosaic and sereh. In habit they have the characteristics of both parents. The thickness of the stalk approaches that of the noble parent. They are not of commercial value because the sugar content is still too low. However, the plants have proved to be of great value in further breeding work (P. O. J. 2364, 2354, 2323).

The reduction division of these plants is more irregular than in the case of the first back-cross, or first nobilization. Thus, in P. O. J. 2364 the number of univalent chromosomes fluctuates between 16 and 26. Therefore, the chromosome number of the sexual cells deviates considerably from the expected monoploid number, 74. When P. O. J. 2364 is crossed with noble cane, the number of somatic chromosomes in the seedlings will range from 106 to 120. The number oscillates around an average of 114, which is equal to the sum of the monoploid chromosome number, 74 of P. O. J. 2364 and 40 of the noble cane. Here, then, there is no doubling of the noble chromosomes.

This cross has produced very valuable seedlings that are outstanding commercial canes (P. O. J. 2714, 2725, 2878, 2883). The most important one of this group is P. O. J. 2878. The seedlings are very vigorous and produce a very high yield of sugar per unit area. They are not immune to mosaic and sereh, but they are very resistant, seldom taking the disease, so that they have sufficient resistance for commercial purposes. It is probable that these canes have about 14 wild (*S. spontaneum*) chromosomes.

If the seedlings of the third nobilization are again crossed to noble cane, the resulting progeny will have a fair sugar yield, but they are more susceptible to mosaic and sereh—or at least some of them are. The chromosome number of the seedlings ranges from 94 to 100, which is the sum of the monoploid numbers of the parents. Others have from 120 to 126 chromosomes, which is about 20 to 30 more than the sum of the monoploid numbers of the chromosomes of the parents. These forms have about seven *S. spontaneum* chromosomes. Apparently as the number of *S. spontaneum* chromosomes is reduced, the seedlings become more susceptible to disease. Because of the irregularity of the reduction division and nonconjunction of chromosomes, there is of course no certainty about the number of wild chromosomes in the individuals of the successive back-crosses. It is striking, however, to notice that a decrease in the number of *S. spontaneum* chromosomes goes hand in hand with greater susceptibility to disease, and it is rather certain that the *S. spontaneum* chromosomes carry the factors that determine immunity to mosaic and sereh diseases.

Effects of Successive Back Crosses

It may be well to summarize briefly the behavior of chromosomes in a species cross and the successive back-crosses. In crossing *S. officinarum* with *S. spontaneum* Java, the diploid number of chromosomes of the hybrid is not equal to the sum of the monoploid numbers of the parents, but the somatic chromosome number of the hybrid, 136, is due to the doubling of the monoploid chromosomes (40×2) of the noble cane together with the 56 chromosomes of the wild cane. In back-crossing the hybrids to *S. officinarum*, the resulting individuals possess 148 somatic chromosomes. Here there is again a doubling of the chromosomes of the noble variety. The number 148 is the sum of twice the monoploid number (40×2) of *S. officinarum* and the haploid chromosome number, 68, of the F_1 hybrid. When the seedlings of the third nobilization are back-crossed to noble cane, there is no doubling of chromosomes. The seedlings of the third and fourth back-cross have a chromosome number that corresponds with the sum of the monoploid chromosomes of the parents, or a slightly larger number.

In the discussion thus far, crosses in which noble canes were used as females have been used to illustrate the behavior of chromosomes in species hybrids. The reciprocal crosses have not been made very often because the F_1 hybrids are very rarely completely pollen sterile. When a pollen sterile individual is found, it can be used as a female in a cross with *S. spontaneum*. The plants resulting from such a cross strongly resemble *S. spontaneum*, forming long stolons, just as *S. spontaneum* does. Stolons do not occur in *S. officinarum* or in the F_1 plants from crosses of *S. officinarum* \times *S. spontaneum*. The F_1 female has about 68 monoploid chromosomes and the male *S. spontaneum* has 56. The seedlings from this cross have 123 or 124 somatic chromosomes. The number equals the sum of the monoploid numbers of the parents. Therefore, when an F_1 individual of *S. officinarum* \times *S. spontaneum* is back-crossed to *S. spontaneum*, doubling of chromosomes does not take place.

Now if a female F_1 is back-crossed to a male noble cane, the individual will have a somatic chromosome number varying from 124 to 138—numbers that are usually larger than the sum of the monoploid

chromosome numbers of the parents, but considerably smaller than the monoploid number of the F_1 plus the diploid number of the noble cane. Thus, the behavior of chromosomes in the crosses (*S. officinarum* \times *S. spontaneum*) \times *S. spontaneum* and (*S. officinarum* \times *S. spontaneum*) \times *S. officinarum* is quite different from the behavior in the reciprocal crosses, where there is a doubling of *S. officinarum* chromosomes.

Hybrids with Larger Chromosome Numbers

Hybrids with a somatic chromosome number greater than 148 have been produced. If one of the seedlings of the third nobilization, that is, P. O. J. 2725, with 108 somatic chromosomes, is crossed with *S. spontaneum* Java, the individuals of the progeny will have about 162–164 chromosomes. This number results from the doubling of the monoploid number of P. O. J. 2725 (54×2) together with the monoploid number of *S. spontaneum* (56). These forms are very robust, resembling in general the F_1 plants of *S. officinarum* \times *S. spontaneum*. They are of no commercial value, but no doubt they will be very valuable in further breeding. By back-crossing hybrids of the third and fourth nobilization, it may be possible to produce commercial sugarcanes with higher chromosome numbers, greater vigor, and higher production of sugar.

We have noticed that when *S. officinarum* is crossed with *S. spontaneum* of Java, there is a doubling of the chromosomes of *S. officinarum*. The same thing happens when noble cane is crossed with other forms of *S. spontaneum*, but, of course, the somatic number of chromosomes of the progeny may not be the same. If noble cane is crossed with *S. spontaneum* Tabongo, which has 40 monoploid chromosomes, the progeny will have 120 somatic chromosomes, and if the cross is with *S. spontaneum* of India, with 32 monoploid chromosomes, the progeny will have 112 somatic chromosomes.

It may also be of interest to note the chromosome numbers of individuals derived from a cross of two forms of *S. spontaneum*. *S. spontaneum* Tabongo, with 40 monoploid chromosomes, was crossed with *S. spontaneum* Kepandjen, with 56 monoploid chromosomes. The hybrids have 96 chromosomes. The reduction division is regular, the chromosomes forming 48 pairs. Apparently, the chromosomes from the different lines of descent pair among themselves. The F_1 individuals are fertile, and no doubt they will breed true in subsequent generations because there would be no segregation of characters, and the chromosome number would remain constantly 96.

The F_1 progeny of *S. officinarum* \times *S. spontaneum* Tabongo are immune to mosaic, but some of the F_1 seedlings of *S. officinarum* \times *S. spontaneum* of Coimbatore are susceptible but rather tolerant.

Species Crosses with *Saccharum robustum*

When *S. officinarum* is crossed with *S. sinense* or *S. barberi*, the monoploid chromosome number of the noble parent is doubled. In the cross *S. barberi* \times *S. spontaneum* of India there is no duplication of chromosomes. When a noble cane is crossed with *S. robustum* there is an increase in chromosomes above the number which corresponds to the sum of the monoploid numbers of the parents, but it is considerably less than the sum of the diploid number of *S. officinarum*

and the monoploid number of *S. robustum*. *S. robustum* is a wild species that breeds true from seed. The sugar content of individuals ranges from 4 to 15 percent, the higher figure approaching that of the noble varieties. The stalks are much larger than those of the *S. spontaneum* forms and its flowers are indistinguishable from those of *S. officinarum*. From a morphological point of view it is much nearer to the noble varieties than are the forms of *S. spontaneum*.

Seedlings from two crosses with noble varieties, D-74 \times *S. robustum* and Simpson \times *S. robustum*, have been studied cytologically. The seedlings from the cross D-74 \times *S. robustum* had 100 somatic chromosomes. The cross Simpson \times *S. robustum* produced viable seed; however, in a total of 689 plants, 680 were albinos and only 9 were green. The albino plants died when they were about 2 weeks old, so their chromosome numbers were not determined. The green plants have about 98 chromosomes. The F₁ seedlings are intermediate in character. The diameter of stalks exceeds that of either parent and the length of stalk approaches that of *S. robustum*. The seedlings are susceptible to mosaica.

The behavior of *S. robustum* with noble canes is somewhat similar to that of *S. spontaneum* with noble canes, but the number of chromosomes duplicated is not so large. The monoploid number of chromosomes of the noble varieties is 40 and that of *S. robustum* 42. As noted, the hybrids of D-74 by *S. robustum* have 100 somatic chromosomes, and the green individuals of Simpson \times *S. robustum* have 96 to 98 chromosomes instead of 82, which is the sum of the monoploid numbers of the parents. Apparently, there is an increase of 16 to 18 chromosomes. This probably indicates that the noble varieties and *S. robustum* have several homologous chromosomes, or at least chromosomes similar enough to pair, and there is a duplication of a few dissimilar chromosomes of each variety. These duplicated chromosomes from different lines of descent pair among themselves. The chromosome complex of the hybrids may be represented as follows: 32 chromosomes of D-74 pair with 32 homologous chromosomes of *S. robustum*; the remaining 8 chromosomes of D-74 are duplicated and the resulting homologous chromosomes pair among themselves; the remaining 10 chromosomes of *S. robustum* do likewise. $(32 + 32 + (8 \times 2) + (10 \times 2) = 100$.

There is the alternative possibility that the increase in chromosomes is due to nonconjunction in the reduction division of the parents, resulting in the formation of gametes with deviating chromosome numbers. The reduction division of the parents, however, is regular, so it is very probable that the gametes have the normal monoploid number. Besides, all the F₁ seedlings studied have the same chromosome number, which would not be the case if the increase were due to aberrant gametes. It seems more probable, therefore, that some of the chromosomes of each parent have doubled—but this does not preclude other explanations.

The chromosome number of the hybrids between *S. officinarum* and *S. robustum* is of significance in connection with the chromosome numbers of many original sugarcane varieties from New Guinea. Most of these New Guinea varieties have morphological characteristics like those of *S. officinarum*, but a great many also have some characteristics of *S. robustum*. The chromosome numbers of 152 of these varieties have been determined. When the varieties are grouped according to chromosome number, it is found that 13.16 percent have

about 80 somatic chromosomes, the characteristic number of *S. officinarum*; 70.39 percent have about 100 somatic chromosomes, the same number as the hybrids of *S. officinarum* \times *S. robustum*; and 16.45 percent have somatic chromosome numbers from 110 to 149. The morphological characteristics and the chromosome numbers of many original New Guinea varieties indicate rather definitely that they are hybrids of *S. officinarum* \times *S. robustum*.

Chromosome Behavior of Generic Hybrids

In the generic cross *S. officinarum* \times *Erianthus*, the sugarcane E. K. 28, with 40 monoploid chromosomes, was the female, and *Erianthus sara*, with 30 monoploid chromosomes, was the male parent (15). The hybrid plants had 60 to 68 chromosomes, a number which was less than the sum of the monoploid numbers of the parents. The reduction division of E. K. 28 was slightly irregular so there is a possibility that gametes were produced which deviated slightly from the monoploid number 40, in both a positive and a negative direction. The reduction division of *E. sara* is very regular and it is highly probable that all the gametes have 30 chromosomes. Gametes of E. K. 28 with less than the haploid number (30–38) probably have a greater chance to form viable zygotes in combination with gametes of *E. sara* than gametes with exactly the monoploid number or with a slightly larger number. The question why the number of chromosomes of *S. officinarum* was not doubled in the case of these hybrids, while such doubling occurred in the cross of *S. officinarum* and *S. spontaneum*, needs thorough investigation.

The reduction division of the F_1 hybrids is rather irregular, the number of univalent and lagging chromosomes varying from 6 to 14. Therefore, most of the hybrid individuals are pollen-sterile; a minority yield a small percentage of fertile pollen. Nothing is known about the behavior of the chromosomes from the different lines of descent. A correct interpretation of these phenomena will be possible only after continued investigation.

There is only fragmentary knowledge concerning the behavior of the chromosomes of sugarcane-sorghum hybrids. The individuals that have been studied are hybrids of P. O. J. 2725, with 53–54 monoploid chromosomes, and *Sorghum durra*, with 10 monoploid chromosomes. The diploid chromosome numbers of the F_1 seedlings fall into three rather definite groups—64, 74, and 116. The number 64 is the sum of the monoploid numbers of the parents; the number 74 is the sum of the diploid number of sorghum and the monoploid number of sugarcane; and the number 116 arises from the doubling of the sugarcane chromosomes, plus the monoploid number of the sorghum chromosomes. The reduction division of the F_1 individuals is very irregular so that the chromosome counts vary considerably. So far as known, all the hybrids are pollen-sterile, and only a very few fertile eggs are produced. Back-crosses of F_1 individuals to sugarcane have not produced viable seeds. Venkatraman obtained a few plants from the back-cross of an F_1 hybrid to sorghum. One of these back-cross plants has about 74 somatic chromosomes. Since the chromosome number of the F_1 plant used in the cross is not known, it is impossible to postulate the behavior of the chromosomes in the back-cross. Further investigation of these very interesting crosses is being carried on, and no doubt interesting and valuable information will be obtained.

LITERATURE CITED

- (1) BACON, Sir F.
1627. THE NEW ATLANTIS. 2 pts. London. [Published after authors death.]
- (2) BARBER, C. A.
1916. THE CLASSIFICATION OF INDIGENOUS INDIAN CANES. Agr. Jour. India 11: 371-376.
- (3) ———
1919. STUDIES IN INDIAN SUGAR CANES, NO. 4. TILLERING OR UNDERGROUND BRANCHING. India Dept. Agr. Mem., Bot. Ser. 10: [39]-153, illus.
- (4) BRANDES, E. W.
1929. INTO PRIMEVAL PAPUA BY SEAPLANE . . . Natl. Geogr. Mag. 56: 253-332, illus.
- (5) BREMER, G.
1928. DE CYTOLOGIE VAN HET SUIKERRIET. DE BIJDRAGE. EEN CYTOLOGISCH ONDERZOEK DER BASTAARDEN TUSSCHEN SACCHARUM OFFICINARUM EN SACCHARUM SPONTANEUM. Arch. Suikerindus. Nederland. Indië, Meded. Proefsta. Java-Suikerindus. 1928 (deel 3): [565]-696, illus.
- (6) ———
1931. DE CYTOLOGIE VAN HET SUIKERRIET. 6DE BIJDRAGE. EEN CYTOLOGISCH ONDERZOEK VAN EEN AANTAL OORSPRONKELIJKE BRITSCH-INDISCHE SUIKERRIETSSOORTEN. Arch. Suikerindus. Nederland. Indië, Meded. Proefsta. Java-Suikerindus. 1931 (deel 3): [1349]-1391, illus.
- (7) ———
1932. ON THE SOMATIC CHROMOSOME NUMBERS OF SUGAR-CANE FORMS AND THE CHROMOSOME NUMBERS OF INDIGENOUS INDIAN CANES. 4th Cong. Internatl. Soc. Sugar Cane Technol. Proc., Bull. 20, 3 pp.
- (8) ———
1934. DE CYTOLOGIE VAN HET SUIKERRIET. 7DE BIJDRAGE EEN CYTOLOGISCH ONDERZOEK VAN EEN VIJFTIGTAL IN 1929-1930 OP JAVA GEIMPORTEERDE RIETSOORTEN. Arch. Suikerindus. Nederland. Indië, Meded. Proefsta. Java-Suikerindus. 1934 (deel 2): 141-166, illus.
- (9) FLEISCHMANN, C. L.
1849. [CULTURE OF SUGARCANE AND MANUFACTURE OF SUGAR.] Commr. Patents Ann. Rept. 1848 (App. 2): 274-338. (30th Cong., 2d sess., Ex. Doc. 59).
- (10) LABAT, J. B.
1722-24. NOUVEAU VOYAGE AUX ISLES DE L'AMERIQUE . . . AVEC UNE DESCRIPTION EXACTE & CURIEUSE DE TOUTE CES ISLES . . . 6 v. La Haye and Paris.
- (11) LIPPMAHN, E. O. VON
1929. GESCHICHTE DES ZUCKERS SEIT DEN ÄLTESTEN ZEITEN BIS ZUM BEGINN DER RÜBENZUCKER-FABRIKATION; EIN BEITRAG ZUR KULTURGESCHICHTE. 824 pp., illus. Berlin.
- (12) McINTOSH, A. E. S.
1932. AN INVESTIGATION INTO THE EVOLUTION OF SUGAR CANE VARIETIES BY BREEDING IN BARBADOS 1887-1925 WITH A DISCUSSION ON THE APPLICATION OF THE FINDINGS TO THE PRESENT DAY SCHEME OF WORK. Barbados Dept. Sci. and Agr. Agr. Jour. 1 (1): 3-17.
- (13) MANGELSDORF, A. J., and LENNOX, C. G.
1932. THE 1930-1931 CROSSING SEASON. SULPHUROUS ACID CROSSES. Hawaii. Sugar Planters' Assoc. Proc. Ann. Meeting (1931) 51: 653. (Director's Rept., p. 93.)
- (14) POSTHUMUS, O.
1930. THE PRESENT STATE OF CANE-BREEDING IN JAVA. 3d Cong. Internatl. Soc. Sugar Cane Technol. Proc. 1929: 420-429.
- (15) RUMKE, C. L.
1934. SACCHARUM-ERIANTHUS BASTAARDEN. Arch. Suikerindus. Nederland. Indië, Meded. Proefsta. Java-Suikerindus. 1934 (deel 2): 211-263, illus.

- (16) THOMAS, R., and VENKATRAMAN, T. S.
1930. SUGAR-SORGHUM HYBRIDS. Agr. Jour. India 25: 164.
- (17) VENKATRAMAN, T. S.
1930. SUGARCANE BREEDING—ITS CHIEF CHARACTERISTICS. Reprinted from Madras Agr. Jour. sec. 5, p. 2, illus.
- (18) ——— and RAO, U. V.
1928. COIMBATORE SEEDLING CANES. (CO'S 205, 210, 213, 214, AND 223 DESCRIBED AND ILLUSTRATED.) Agr. Jour. India 23: 28–38, illus.
- (19) VERRET, J. A., in collaboration with KUTSUNAI, Y., DAS, U. K., CONANT, R., and SMITH, T.
1925. A METHOD OF HANDLING CANE TASSELS FOR BREEDING WORK. Hawaii Planters' Rec. 29: 84–94, illus.
- (20) WILLIAMS, F. E.
OROKAIVA MAGIC CAMBRIDGE UNIVERSITY PRESS, 1928 ALSO ANTHROPOLOGY REPORTS, TERRITORY OF PAPUA, PORT MORESBY.
- (21) WRAY, L.
1848. THE PRACTICAL SUGAR PLANTER; A COMPLETE ACCOUNT OF THE CULTIVATION AND MANUFACTURE OF THE SUGAR-CANE, ACCORDING TO THE LATEST AND MOST IMPROVED PROCESSES . . . 415 pp., illus. London.

Appendix

TABLE 3.—*Natural species and some natural varieties of sugarcane*

Species and variety	Sex	Somatic chromo- some	Parents	Origin	Important characters	Commercial planting
		<i>Number</i>				
<i>S. officinarum</i> L.		80		Natural		
Black Cheribon	Female	80		do.		
Gestreet Preanger	do.	80		do.		
Batjam	Male	80		do.		
Bandjarmasin hitam	Female	80		do.		
Fiji	do.	80		do.		
Crystalina	do.	80		do.		
Otaheite	do.	80		do.		
Badila	Female and male	80		do.		
Yellow Caledonia	Female			do.		
Loethers (hybrid?)	Male	98-99		do.		
Creole (hybrid?)		81		do.		
Naz (Reunion) (hybrid?)		100-110		do.		
Uba Marot (hybrid?)	Male	113		do.		
Kara Kara Wa (hybrid?)		124-125		do.		
<i>S. sinense</i> Roxb.		116-118		do.		
Kavengirie		118		do.		
Uba	Female	116-118		do.		
Cayana	do.	116-118		do.		
<i>S. barberi</i> Jeswiet:						
Sunnabile group		116		do.		
Dhault group		82		do.		
Mungo group		82		do.		
Nagori group		124		do.		
Hybrids		107		do.		
Saretha group		90-92		do.		
Chunnee group		90-91		do.		
<i>S. spontaneum</i> L.	Male			do.		
Pasoeroean and Java forms.	do.	112		do.		
Tabongo	do.	80		do.		
Biroh group	do.	96		do.		
Burma group	do.	96		do.		
Krakatau	do.	124		do.		
Tananggé	do.	60		do.		
Dacca	do.	78		do.		
Coimbatore	do.	64		do.		

Most of the varieties of *S. officinarum* formerly were of high commercial value. At present most of the varieties are no longer grown commercially. The few that remain, Crystalina, Yellow Caledonia, Badila, etc., are being replaced by superior hybrid seedlings.

Being replanted by superior seedlings. Still used in Natal, Brazil, and parts of Hawaii.

Formerly the commercial canes of India; now largely replaced by superior hybrid varieties.

No commercial value.

Sumatra, thin stemmed	do	108	do		
Sumatra, thick stemmed.	do	128	do		
Dehra Dun	do	54	do		
<i>S. robustum</i> (?)	do	84	do	Great vigor; high fiber; range, tropical.	Do.
Self-seedlings		76-84	do	do	Do.
Natural species hybrids: Kassoer	Male	136	<i>S. officinarum</i> (Black Cheribon) × <i>S. spontaneum</i> Java.	Immune to mosaic and serah; high fiber; great vigor.	Do.
Toledo	do	120	<i>S. officinarum</i> × <i>S. spontaneum</i> Tabongo.	do	Do.
Hinds Special	do	120	do	do	Do.

Most of the hybrid seedlings produced the world over are from combinations of the natural varieties and the following hybrids: P. O. J. 100; S. W. 499; E. K. 2, 28; 247B, P. O. J. 2364, 2725, 213, 2878, and 36; Co. 213, 214, 281, and 290; D. 74, 625; Diamond 10; T. 24; S. C. 12/4; B. H. 10/12; Ba. 11569; U. S. 1694; C. P. 1165, 1161; H. Q. 409.

TABLE 4.—*Characteristics of elite breeding stock and commercial seedlings derived from this stock*

Source and variety	Sex	Origin	Parents	Important characters	Commercial plantings			Date bred	Breeder
					In-creas-ing	De-creas-ing	Dis-con-tinued		
Africa:									
E-8		Egypt (seed imported from Hawaii).	U. S. 666 selfed	Tolerant to streak disease.	(1)			1928	A. J. Mangelsdorf.
M-131	Female	Mauritius	P. O. J. 2725 × Uba Marot.	Rapid growth; high sucrose.	(1)				D. d'Emmerez de Charmoy. Do. Do
R-11	Male	Reunion	P. O. J. 2725 × D-74	Mosaic resistant; drought resistant; early maturity.	(1)				
R-54		do	P. O. J. 36 × Uba Marot	High sucrose; early maturity.	(1)				
R-157		do		Resistant to mosaic, gummosis, and rust; high fiber; sugar low; very vigorous.					
Uba Marot	Male	Natural		Mosaic and drought resistant; vigorous.					
Guingham	Female	do		High sucrose; drought resistant.		×			
Isautier		Reunion	Unknown				×	1889	Dumesnil.

See footnotes at end of table

TABLE 4.—*Characteristics of elite breeding stock and commercial seedlings derived from this stock—Continued*

Source and variety	Sex	Origin	Parents	Important characters	Commercial plantings			Date bred	Breeder
					In- creas- ing	De- creas- ing	Dis- con- tinued		
Asia:									
Co. 205	Male	India (Coimbatore)	Vellai × <i>S. spontaneum</i> India.	Coimbatore seedlings are in general very vigorous; early maturing; tolerant of mosaic; immune to sereh. Co. 281 resistant to red rot (La.).		×		1914	C. A. Barber.
Co. 206	do	do	Ashy Mauritius × <i>S. spontaneum</i> India.					1914	Do.
Co. 213	Female	do	P. O. J. 213 × Kansar			×		1914	Do.
Co. 214	do	do	Striped Mauritius × M 4600.					1914	Do.
Co. 221	Female	do	P. O. J. 213 × Co. 291					1918(?)	T. S. Venkatraman.
Co. 229	do	do	Co. 205 selfed						Do.
Co. 243	do	do	A 2 × Co. 206						Do.
Co. 244	do	do	P. O. J. 213 × Co. 205						Do.
Co. 281	Female	do	P. O. J. 213 × Co. 206		×				Do.
Co. 285	do	do	Striped Mauritius, Green Sport × Co. 205 (?)		×				Do.
Co. 221	do	do	Co. 221 × D-74(?)						Do.
Co. 290	Male	do			×				Do.
Co. 299	do	do							Do.
Co. 300	do	do							Do.
Co. 312	Male	do							Do.
Co. 313	do	do	Co. 213 × Co. 244						Do.
Co. 326	do	do	Co. 229 selfed						Do.
Co. 331	do	do	Co. 213 × Co. 214		×				Do.
Co. 347	do	do	Co. 281 × Co. 223						Do.
Co. 349	do	do	P. O. J. 2725 × Co. 243						Do.
Co. 350	do	do	Co. 213 × Co. 281						Do.
Co. 351	do	do	P. O. J. 2725 × <i>Sorghum durra</i> .					1929	Do.
Co. 352	do	do	do					1929	Do.
Co. 357	do	do	do					1929	Do.
Co. 402	do	do	Vellai × Co. 243						Do.
Co. 408	do	do	P. O. J. 2725 × Co. 243						Do.
Australia and Fiji:									
18 R 1167		Fiji	H 109 × unknown	Resistant to Fiji disease.		×		1918	W. A. Speight.
H. Q. 409 (Clark's seedling).		do	87 Couvé × unknown	Resistant to gumming disease.		×		1904	Do.
H. Q. 406		do	Goru × unknown	High quality and tonnage.		×		1904	Do.
Broadwater 1		do	Korpi × unknown	Resistant to gummosis.		×		1922	D. S. North.
J. S. 2		Queensland	Badila	High quality and vigor but susceptible to mosaic, gumming, and Fiji disease.			×	1922	McWalters.

J. S. 4		do	do	do			×	1922	Do.
J. S. 7		do	do	do			×	1922	Do.
H. Q. 285		do	N. G. 24	Early maturity			×	1905	James Clark.
H. Q. 426		do	do	do			×	1905	Do.
H. Q. 409	Male	do	do	Early maturity, vigor			×	1905	Do.
H. Q. 458		do	do	Disease resistant			×	1905	Do.
Q. 813	Male	do	Badila	do			×	1900	W. Mitchell.
Q. 1098		do	do	do			×	1910	Do.
N. G. 15	Female and male.	Natural		High sucrose					
N. G. 24	Male	do		do					
Orambo	Female	do		do					
S. J. 684a	do	Queensland		High sucrose, vigor					E. J. Barke.
S. J. 642c	Male	do		Vigor					Do.
S. J. 672b	do	do	Badila × S. C. 12/4	High sucrose, vigor					Do.
S. J. 274a	do	do		Vigor					Do.
S. J. 662b	do	do		do					Do.
S. J. 848a	Female	do		do					Do.
S. J. 267a	Male	do	Rose Bamboo × S. C. 12/4	do					Do.
Q. 3		do	P. O. J. 2878 × S. J. 86a		(1)				
Q. 4		do	P. O. J. 2878 × S. J. 672b		(1)				
Q. 5		do	P. O. J. 2364 × S. J. 267a		(1)				
Pacific islands:									
Java:									
P. O. J. 36	Female	Java	Gesprept Preanger × Chunnee.	Early maturity, immune to Sereh, mosaic tolerant.	×			1893	J. D. Kobus.
P. O. J. 36-M	do	do	do	do		×		1893	Do.
P. O. J. 105	do	do	do	do		×		1893	Do.
P. O. J. 213	do	do	Black Cheribon × Chunnee.	do		×		1893	Do.
P. O. J. 234	do	do	do	do		×		1893	Do.
P. O. J. 100	do	do	Bandjarasin hitam × Loethers.	High yield		×		1893	J. H. Wakker.
247 B	Male	do	Black Cheribon × Fiji (?)	do		×		1894	R. J. Bouricius.
E. K. 2	do	do	Lahaina × Fiji	do		×			E. Karthaus.
E. K. 28	do	do	E. K. 2 × P. O. J. 100	do		×		1911	J. W. Versteegh.
D. I. 52	do	do	Black Cheribon × Batjam.	do		×		1903	Stok.
S. W. 3	do	do	do	High yield, early		×			Do.
S. W. 111	do	do	do	do		×			Do.
Tjepiring 24	do	do	Black Cheribon × Kassoer.	Immune to mosaic and Sereh, great vigor.		×		1904	G. J. de Kock.
P. O. J. 2364	Female	do	P. O. J. 100 × Kassoer.	do				1911	G. Wilbrink.
P. O. J. 2714	do	do	P. O. J. 2364 × E. K. 28	Resistant to mosaic and Sereh, vigorous.		×		1917	J. Jeswict.
P. O. J. 2725	do	do	do	do	×			1917	Do.
P. O. J. 2722	do	do	do	do				1917	Do.
P. O. J. 2878	Male	do	do	Resistant to mosaic and Sereh, high yield.	×			1921	Do.

See footnotes at end of table.

TABLE 4.—*Characteristics of elite breeding stock and commercial seedlings derived from this stock—Continued*

Source and variety	Sex	Origin	Parents	Important characters	Commercial plantings			Date bred	Breeder
					In-creasing	De-creasing	Dis-continued		
Pacific Islands—Contd.									
Hawaii:									
H. 109.....	Female..	Hawaii	Lahaina × unknown.....	High yield.....		×		1906	C. F. Echart.
H. 456.....	Male.....	do.....	H. 240.....		×			1913	Do.
K. 107.....	do.....	do.....	D. 1135 × unknown.....	Resistant to red stripe and eye spot.	×			1917	W. Twigg-Smith.
K. 202.....	Female..	do.....	D. 1135 × unknown.....	do.....	×			1917	Do.
25 C 14.....	do.....	do.....	Yellow Caledonia × D. 1135.	do.....				1925	A. J. Mangelsdorf.
25 C 34.....	Male.....	do.....	do.....	Eyespot resistant.....				1925	Do.
K. 73.....	do.....	do.....	D. 1135 × unknown.....	do.....				1917	W. Twigg-Smith.
H. 9812.....	do.....	do.....						(1930?)	A. J. Mangelsdorf.
U. D. 1.....	do.....	do.....	Uba × D. 1135.....	Adapted to poor soils.....	×			1924	Hawaiian Sugar Planters Association.
McBryde 7.....		do.....	Lahaina	Long crops, lower fields.....	×			1918	McBryde Sugar Co.
Manoa 213.....		do.....	Tip.....	Middle and Makai lands.....	×			1922	Hawaiian Sugar Planters Association.
Philippines:									
L. C. 25/191 (Aluman).		Philippine Islands.....	Badila × 247 B.....	High yield.....	×			1925	A. Labrador.
P. S. A. 7.....		do.....	P. B. 119 × C. A. C. 87.....	do.....	×			1925	N. B. Mendiola.
P. S. A. 14.....		do.....	do.....	do.....	×			1925	Do.
West Indies:									
Barbados:									
B. H. 10/12.....	Male.....	Barbados.....	Ba 6835 × B. 4578.....	High yield; resistant to gummosis.		×		1910	Department of Agriculture, Barbados.
S. C. 12/4.....	do.....	do.....	do.....	High quality; adapted to West Indies; resistant to gummosis.		×		1912	Do.
B. A. 11569.....	Female..	do.....	B. 16536.....	Adapted to low rainfall.....		×		1911	Do.
B. 417.....	Male.....	do.....	B. 6835.....	High quality; resistant to gummosis.			×	1917	Do.
B. 726.....		do.....	Ba. 11569.....	Adapted to intermediate rainfall; high quality.		×		1922	Do.
B. 2935.....		do.....	Ba. 11569 × Ba. 6032.....	Adapted to low rainfall; resistant to gummosis.	×			1927	Do.
Burke.....		do.....	Unknown.....	General improvement.....			×	Before 1904	Do.
B. 147.....		do.....	do.....	do.....			×	do	Do.
B. 208.....		do.....	do.....	High juice quality.....			×	do	Do.
B. 376.....		do.....	do.....	do.....			×	do	Do.

B. 6308		do.	T. 24	General improvement			×	1903	Do.
B. 6450		do.	do.	do.			×	1903	Do.
Ba. 6032		do.	B. 7169	do.			×	1910	Do.
Puerto Rico:									
Fajardo Sugar Co.:									
F. C. 306		Fajardo	D. 433 × unknown	High yield; susceptible to gummosis and leaf spot.			×	1915	R. A. Veve.
F. C. 436		do.	D. 448 × unknown	do.			×	1918	Do.
F. C. 553		do.	D. 433 × unknown	do.			×	1922	L. de Celia.
F. C. 588		do.	do.	do.			×	1922	Do.
F. C. 668		do.	do.	do.			×	1922	Do.
Mayaguez:							×	1926	R. L. Davis.
Mayaguez 28		Puerto Rican Agricultural Experiment Station.	P. O. J. 2725 × S. C. 12/4	Mosaic resistant; late maturity.					
Mayaguez 63		do.	do.	Resistant to mosaic; poor germination.			×	1926	Do.
North America, U. S. Department of Agriculture, Canal Point, Fla.:									
C. P. 807	Female.	U. S. Department of Agriculture.	U. S. 1643 × unknown	Resistant to mosaic; great vigor; early maturity.		×		1924	E. W. Brandes.
C. P. 27/139	do.	do.	P. O. J. 2725 × U. S. 1694	Resistant to mosaic and adapted to sawgrass muck.		×		1927	P. J. Klaphaak.
C. P. 28/11	do.	do.	Co. 281 × U. S. 1694	Early maturity; resistant to mosaic and red rot.		×		1928	Do.
C. P. 28/19		do.	do.	do.		×		1928	G. B. Sartoris.
C. P. 29/320		do.	Co. 281 × C. P. 27/34	do.		×		1929	Do.
South America, Demerara:									
D. 74		British Guiana Department of Agriculture.	White Transparent	High yield; early maturity.			×	1889	British Guiana Department of Agriculture.
D. 95		do.					×	1889	J. V. Harrison.
D. 109		do.					×		Do. (?)
D. 117		do.					×		Do. (?)
D. 625		do.					×	1892	Do. (?)
D. 1135		do.					×		Do. (?)
D. 4930		do.	D. 625			(1)			British Guiana Department of Agriculture.
D. 66/30		do.	Diamond 10 × S. C. 12/4						Do.
Diamond 10		Diamond Plantation	Unknown			×			Diamond Plantation, British Guiana.
Argentina, Tucuman:									
Tuc. 472		Estacion Experimental Agricola.	do.	Resistant to mosaic and frost; very vigorous; early.		×			W. E. Cross, Estacion Experimental Agricola.

¹ Trial stage.² Inferior to B. H. 10/12.

TABLE 5.—*World stations—past, present, and projected work, personnel, and expenditures*

Country and station	Date established	Seedlings studied	Uncontrolled pollinations	Controlled pollinations	Objective	Method			Commercial seedlings
						Variety crosses	Species crosses	Generic crosses	
West Indies: Barbados-----	1887	Number 200, 000	Number 150, 000	Number 150, 000	Yield quality; resistance to gumming; arrowing sparse or absent.	Ba. 11569 × BH 10/12, Ba. 11569 × B 417, Ba. 11569 × S. C. 12/4, Ba. 11569 × B. 603, Ba. 11569 × Ba. 8069.	<i>S. officinarum</i> × <i>S. spontaneum</i> , <i>S. officinarum</i> × <i>S. sinense</i> , <i>S. officinarum</i> × <i>S. barberi</i> .	-----	B. H. 10/12, S. C. 12/4, B. 726, B. 2935.
Puerto Rico: Fajardo-----	1914	32, 023	9, 353	22, 670	High yield, rapid growth, late or nonflowering, resistance to drought, excessive moisture, mosaic.	-----	P. O. J. 2725 × S. C. 12/4, P. O. J. 2725 × B. H. 10/12, B. H. 10/12 × F. C. 915.	-----	F. C. 306, 915, 916, 1017.
Mayaguez-----	1917	121, 450	2, 500	118, 950	High yield, vigor, sparse flowering, early maturity, shedding of leaves, resistance to mosaic, leaf-spot diseases.	-----	P. O. J. 2725 × S. C. 12/4, P. O. J. 2725 × B. H. 10/12, M. 28 × P. O. J. 2878.	None-----	Mayaguez 28, Mayaguez 63.
Martinique-----		(3)				Ba. 6032 selfed; Martinique 23, 58, 302, 198, 158, 280, 161, 1132; Martinique 23 best.		-----	
Africa: Mauritius and Reunion.	1883	(4)				Guingham × D. K. 74 ⁵ .	M. 131 × D. K. 74, P. O. J. 213 × D. 109, P. O. J. 2725 × D. K. 74, P. O. J. 2725 × Co. 214, P. O. J. 2878 × Isautier (noble), P. O. J. 2878 × Uba Marot, P. O. J. 2878 × D. 96 (P. O. J. 2725 × Uba Marot), P. O. J. 2878 × D. 172 (P. O. J. 2725 × Uba Marot).	-----	Isautier (1889).
Natal-----	1929	(6)							

Egypt-----	1930	(7)					Ba. 11560 × B. H. 10/12, Ba. 11509 × S. C. 12/4, B. A. 11569 × D. 1135, H. Q. 409 × S. C. 12/4 Diamond 10, D. 625 selfed.	U. S. 666 selfed, P. O. J. 2725 × U. S. 666, P. O. J. 2364 × S. C. 12/4, P. O. J. 2878 selfed, Co. 281 selfed, 26-C-148 × Molokai 1694, 28-1681 × 32-7665, Toledo × S. C. 12/4, M. D. 41 × B. H. 10/12, P. O. J. 2725 × S. C. 12/4.		
Reunion ⁸ -----	1889	(4)								
East Indies:-----										
Java-----	1886	(4)					×	Kassoer nobilization <i>S. officinarum</i> × <i>S. spontaneum</i> .	<i>S. officinarum</i> × <i>Eri-anthus sara</i> .	E. K. 2, E. K. 28, 247 B, D. I. 52, Tjepiring 24, S. W. 3, S. W. 111, S. W. 499, P. O. J. 36 and 36-M, P. O. J. 213, 234, 2725, 2878, 2883.
Argentina:-----										
Tucuman-----	1916	2,600	600	2,000	High yield; mosaic-resistance.	H. 109 × Yellow Tip; D. 666/18 selfed, S. C. 12/4 selfed.	H. 109 × P. O. J. 2878, ⁶ P. O. J. 2725 × Manoa 315, Striped Mexican × P. O. J. 2878, Co. 205 selfed, 4473-C selfed.	None-----		Tucuman 472.
Australia:-----										
New South Wales-----	1928	7,400	1,500	5,900	Maturing 14 months; maturing 21 months; resistance to gumming, mosaic, leaf scald, Fiji disease; red rot, root rot "rust"; adapted to alluvial, peat, and poor soils; cold-resistance.		P. O. J. 2364 × 28 M., Q. 417, P. O. J. 2878 × 28 M., Q. 674, P. O. J. 2364 × B. 374, P. O. J. 2878 selfed, <i>S. officinarum</i> × <i>S. robustum</i> , <i>S. officinarum</i> × <i>S. barberi</i> , <i>S. sinense</i> × <i>S. barberi</i> .	---do-----		None.
Queensland-----	1890	200,000	25,000	175,000	Varieties resistant to disease and adaptability to soil and climate of various districts; same diseases as for Australia.	Orambo × H. Q. 409, S. J. 684a × S. J. 642c, N. G. 15 × S. J. 274a, N. G. 15 × S. J. 662b, S. J. 848c × N. G. 15.	P. O. J. 2878 × S. J. 672b, <i>S. officinarum</i> × <i>S. spontaneum</i> , <i>S. officinarum</i> × <i>S. robustum</i> , <i>S. officinarum</i> × <i>S. sinense</i> , <i>S. officinarum</i> × <i>S. barberi</i> .	---do-----		Just commencing to be grown commercially.

See footnotes at end of table.

TABLE 5.—*World stations—past, present, and projected work, personnel, and expenditures—Continued*

Country and station	Date established	Seedlings studied	Uncontrolled pollinations	Controlled pollinations	Objective	Method			Commercial seedlings
						Variety crosses	Species crosses	Generic crosses	
Australia—Con. Fiji and New South Wales.	1913, 1924	Number 57,000	Number 10,000	Number 47,000	Varieties resistant to diseases as listed for Australia and to cane grub, weevil borer. Good ratooning; adapted to soil and climate of various districts.	-----	Crosses of hybrids of the sugarcane species: Badila \times <i>S. robustum</i> ; Korpi \times <i>S. robustum</i> ; Oranhoo \times <i>S. robustum</i> ; F_1 back crossed to noble parent; F_2 back crossed to Badila and Korpi.	28 N. G. 7 (<i>Erianthus</i>) \times Badila.	Broadwater 1, H. Q. 409, H. Q. 426 (Clark's seedling).
Philippine Islands: B. P. I. Manila ¹⁰	1920	316,960	-----	316,960	-----	-----	\times -----	-----	L. C. 25/191 (Aluman), Badila \times 247B.
College of Agriculture, Laguna, P. I.	1919	126,123	¹² 6,956	119,167	High yield; resistance to major diseases of Philippines; adaptability to soil and climate of different districts.	-----	\times -----	None-----	C. A. C. 111, 117, 126, 127, 130; P. S. A. 7, 14.
Hawaii-----	1904	1,000,000	300,000	700,000	High sucrose content; resistance to diseases; rapid closing-in, good weed control. Freedom from tasseling. High yield per unit of time.	Yellow Caledonia \times H-109.	<i>S. officinarum</i> \times <i>S. spontaneum</i> ; <i>S. officinarum</i> \times <i>S. robustum</i> ; <i>S. officinarum</i> \times <i>S. sinense</i> ; <i>S. officinarum</i> \times <i>S. barberi</i> .	Sugarcane \times sorghum; sugarcane \times <i>Erianthus arundinaceum</i> .	H-109, H-146, H-456, K-202, K-107, H-9806, U. D. 1, H-8965, 25 C 28, 28-2055, 28-1234, 28-1864, 31-1389, McBryde 7.
India: Coimbatore-----	1912	(¹³)	(⁴)	(⁴)	Early maturity; resistance to mosaic, red rot, and smut; adapted to various regions of India.	\times -----	<i>S. officinarum</i> \times <i>S. spontaneum</i> India, <i>S. officinarum</i> \times <i>S. barberi</i> .	Sugarcane \times sorghum.	Co. 205, 213, 214, 281, 285, 290, 313, ¹⁴ 331, ¹⁴ 357. ¹⁴

United States: Canal Point, Fla.	1921	150,000	30,000	120,000	Early maturity; high yield; resistance to Mosaic, red rot, adapted to various sugarcane areas of United States.	-----	<i>S. officinarum</i> × <i>S. spontaneum</i> Java, <i>S. officinarum</i> × <i>S. spontaneum</i> India, <i>S. officinarum</i> × <i>S. sinense</i> , <i>S. officinarum</i> × <i>S. robustum</i> , <i>S. officinarum</i> × <i>S. barberi</i> .	-----do-----	C. P. 807, 27-139, 28-11, 28-19, 29-320.
British Guiana: Demerara	1889	(4)	-----	-----	High yield	Nearly all crosses of varieties of noble canes.	Some seedlings from P. O. J. 2725.	-----	D-74, D-95, D-109, D-117, D-433, D-1135, D-625, Diamond 10, D-49/30, ¹⁵ D-66/30. ¹⁵

Country and station	Qualitative characters	Quantitative characters	Theoretical breeding	Cytology (chromosome number and behavior)	Elite breeding stock	Future investigations	Personnel		Annual expenditures
							Early	Present	
West Indies: Barbados	Selfed lines; no results.	Progeny testing, cane number, weight, length, diameter, percent of sucrose.	None	None	Not enough data.	Correlation, growth, types of seedlings to different environments and maturity and soundness of canes in stool during crop.	J. R. Bovell, J. B. Harrison, L. Lewton-Brain, F. A. Stockdale, J. P. d'Albuquerque, L. C. C. Leibenberg, S. H. Evelyn, — Jenman.	A. E. S. McIntosh, G. C. Stevenson.	£5,500
Puerto Rico: Fajardo	None	None	do	do			R. C. McConnie, R. A. Veve, L. de Celia, R. Bermúdez.	J. E. Veve, R. Bird-Acosta.	\$2,500
Mayaguez	do	do	Kassoe selfs; inbreeding.	do		Selfed lines; inheritance of disease; resistance to mosaic; sparse or late arrowing.		R. L. Davis	
Martinique							— Littée	E. Bassières	
Africa: Mauritius and Reunion.					D. K. 74 ¹ , M. 131, Uba Marot.		Dumesnil, Boname, Perromat.	D. d'Emmerez de Charmoy.	Fr.100,000
Natal									H. H. Dodds
Egypt							P. Neuville	H. H. Rosenfeld.	
Reunion ⁸								D. d'Emmerez de Charmoy.	

See footnotes at end of table.

TABLE 5.—*World stations—past, present, and projected work, personnel, and expenditures—Continued*

Country and station	Qualitative characters	Quantitative characters	Theoretical breeding	Cytology (chromosome number and behavior)	Elite breeding stock	Future investigations	Personnel		Annual expenditures
							Early	Present	
East Indies: Java.....	Selfed lines discontinued.	General characteristics of progeny from certain parents.		Varieties of all species and numerous hybrids.	P. O. J. 100, E. K. 28, Kassoe, P. O. J. 2364.		J. D. Kobus, Krüeger, W. Moquette, J. H. Wakker, Soltwedel, J. W. Versteegh, R. J. Bouricius, J. G. de Kock, J. P. Bannier, E. Karthaus, G. Wilbrink, J. Jeswiet.	O. Posthumus.	
Argentina: Tucuman.....								W. E. Cross.	
Australia: New South Wales.....						Stalk size; disease resistance; cytology of species and hybrids.		H. Wenholtz, W. H. Darragh.	£1, 500
Queensland.....						"Pure" lines; disease resistance and vigor.	W. Mitchell.	A. F. Bell, E. J. Barke.	£1, 200
Fiji and New South Wales.			Selfed lines, showed no promise, discontinued.			Correlation of seedling and mature cane characters.	James Clark, W. A. Speight.	H. F. Clarke, J. Trivett, K. R. Gard, D. S. North.	
Philippine Islands: B. P. I. Manila ¹⁰ College of Agriculture, Laguna, P. I.	Anther color and pollen fertility.	Diameter, length, and number of stalks; cane tonnage; sugar yield.	Six types isolated from Badilla selfed seedlings.				A. Labrador.	None.	\$2, 500
								N. B. Mendiola, T. Mercado, J. M. Capenpin.	

Hawaii-----	Eyespot resistance.	Studies on inheritance of sucrose content.		X-----		Mass fertilization; inheritance of sucrose content and resistance to more important diseases.	C. F. Echart, W. Twigg-Smith, Y. Kutsunai, J. A. Verret, W. W. G. Moir, H. P. Agee, W. P. Naquin, W. C. Jennings, W. P. Alexander, C. F. Poole, Raymond Conant, J. A. H. Wilder, J. S. B. Pratt, Jr., E. G. Clark, G. C. Watt, J. N. P. Webster.	A. J. Mangelsdorf, C. G. Lennox, A. D. Waterhouse, Douglas Thomas.	
India: Coimbatore-----					Co. 205, 206, 213, 221, 231, 290, 312, 313, P. O. J. 213, P. O. J. 2725, P. O. J. 2878, 247 B.		C. A. Barber-----	T. S. Venkatraman, N. L. Dutt.	
United States: Canal Point, Fla.---	Inheritance of resistance to mosaic and red rot.	Early maturity and yield.	<i>S. officinarum</i> × <i>S. spontaneum</i> inheritance of mosaic.		U. S. 1643, C. P. 1165, 1161, P. O. J. 2725, 2878, Co. 281, C. P. 29-290, 27-108.	Cytology; inheritance of disease resistance; progeny testing.	E. W. Brandes, P. J. Klappaak, B. A. Bourne.	G. B. Sartoris, J. W. Strickland, R. T. Gibbens, Jr.	
British Guiana: Demerara-----					D-625, D-145, Diamond 10, D-238/17, S. C. 12/4, P. O. J. 2725.		J. B. Harrison, — Jenman.	C. H. B. Williams, R. R. Follett-Smith, C. Cameron.	

¹ Date begun, 1922.² Date begun, 1926.³ Produced a few seedlings.⁴ Numerous.⁵ D. K. 74. = D. 74.⁶ Seed imported.⁷ Seed imported from Hawaii, United States, Barbados, Mauritius, Puerto Rico, Demerara, and Queensland.⁸ Discontinued soon after started. Work renewed recently. See Mauritius.⁹ Discontinued, 1928.¹⁰ Work discontinued 1932.¹¹ Salaries and wages not included.¹² Discontinued.¹³ Many thousands.¹⁴ Experimental stage.¹⁵ New seedlings showing great promise.

